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Fishery Bulletin

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Fishery Bulletin

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REVISION OF THE SAURIES (PISCES, SCOMBERESOCIDAE) WITH DESCRIPTIONS OF TWO NEW GENERA AND ONE NEW SPECIES

CARL L. HUBBS AND ROBERT L. WISNER[1]

ABSTRACT

The extant members of the Scomberesocidae are: 1) *Scomberesox saurus saurus* of the North Atlantic, ranging into the Arctic north of Europe, and *Scomberesox saurus scombroides*, of disjunct occurrence in the Southern Hemisphere; and 2) *Cololabis saira* of the North Pacific (with one record attributed to release of bait in the Indo-Pacific tropics), two dwarf species, *Nanichthys simulans*, new genus and species, of the central Atlantic and the Indian Oceans, and *Elassichthys* (new genus) *adocetus*, of the eastern central Pacific. Some other names applied to Miocene fossils from southern California have been referred, we believe erroneously, to the Scomberesocidae. *Elassichthys adocetus* is particularly dwarfed but both dwarfs are distinguished by having no gas bladder and by having a single ovary which, at maturity, very largely fills the body cavity with few large ova. All members of the group are epipelagic, and they constitute a major element of that assemblage over a large share of the tropical and temperate world ocean.

Fishes of the family Scomberesocidae form a well-defined unit, due principally to the presence of separated finlets posterior to the dorsal and anal fins (as commonly found in scombroid fishes) and in having a slender, pikelike body with these median fins set far back (Figure 1). We interpret the scomberesocids as more or less akin to the Belonididae, Hemiramphidae, and Exocetidae, largely on the basis of having the lower pharyngeal bones united, and the lateral line low, near the ventral profile, rather than (as in most fishes) high on the lateral aspect of the body.

The ordinal classification of the family has been variously interpreted since the turn of the century. For example, it was placed in a division called the "Scombresocidae microsquamatae" by Schlesinger (1909); in the subfamily Scomberesocinae of the Exocoetidae by Regan (1911); in the family Scomberesocidae of the order Synentognathi by Jordan (1923) and by others of his school; in the Scomberesocidae of the suborder Microsquamati of the order Synentognathi by Nichols and Breder (1928); in the suborder Scomberesocoidei, including also the Belonidae, in the Beloniformes by Berg (1940); and, more recently, in the family Scomberesocidae of the superfamily Scomberesocoidea in the suborder Exocoetoidei and order Atheriniformes by Rosen (1964) and by Greenwood et al. (1966), who deleted the superfamily. Bailey et al. (1970) in general followed Greenwood et al., as did Nelson (1976). Gosline (1971) preferred to recognize the order Beloniformes, suborder Scomberesocoidei, families Scomberesocidae and Belonidae, and suborder Exocoetoidei, families Exocoetidae and Hemiramphidae; Gosline did not refer to Greenwood et al. (1966). Despite varied opinions on the ordinal level, all authors retained the scomberesocid fishes as a familial unit.

The Scomberesocidae appear to comprise a compact group to which we add two new genera and one new species. The genera and their species are characterized in Table 1. *Scomberesox* and *Cololabis* are relatively large fishes (about 350-450 mm), have paired ovaries and a gas bladder, while *Elassichthys* and *Nanichthys* are dwarfed (not known to exceed 126 mm, and one species not exceeding 68 mm standard length (SL)), have a single ovary, and lack a gas bladder. Also, they have fewer pectoral and procurrent caudal fin rays, gill rakers, and vertebrae.

Several of the authorities cited above, and others, have indicated that the Scomberesocidae represent an evolutionary line highly specialized for active life at the surface. The modifications of the posterior dorsal and anal rays into finlets, as in various scombroids, is evidence for this view. As a corollary, it seems obvious that a strong swimmer like *Cololabis saira* or *Scomberesox saurus*, rather than the smaller, probably weaker *Elassichthys*

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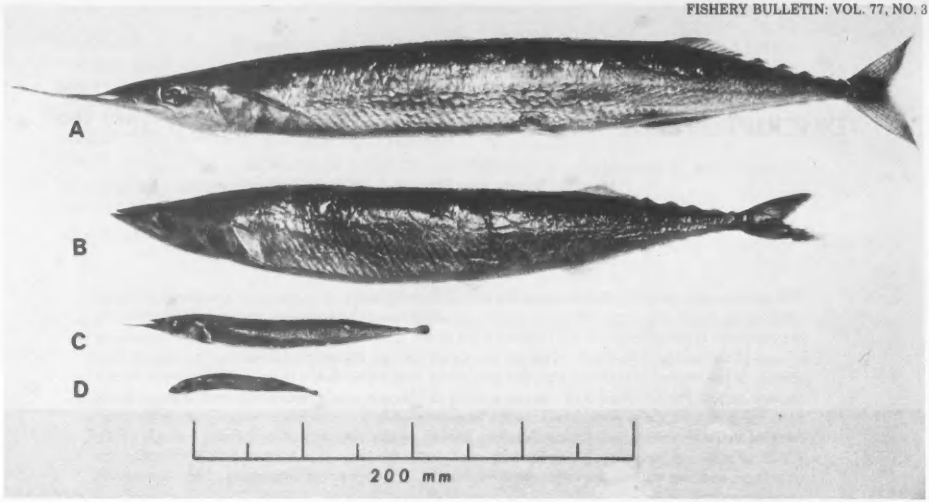

FIGURE 1.—Adults of the four genera and species of scomberesocid fishes: (A) *Scomberesox saurus*; B *Cololabis saira*; (C) *Nanichthys simulans*; (D) *Elassichthys adocetus*.

TABLE 1.—Differential characters of the four genera and species of Scomberesocidae.

Characters	*Cololabis saira*	*Scomberesox saurus*[1]	*Nanichthys simulans*	*Elassichthys adocetus*
Ovaries (Figure 8)	Paired; bilateral	Paired; bilateral	Single; median	Single; median
Testes (Figure 9)	Paired, bilateral; neither overtopping other	Paired, bilateral; neither overtopping other	Paired but forming coherent mass; left overtopping right	Paired but forming coherent mass; left overtopping right
Gas bladder	Large; thin-walled	Large; thin-walled	Completely lacking	Completely lacking
Maximum known length	Ca. 400 mm	Ca. 450 mm	68 mm	126 mm
Developed gonads	Dorsolateral to gut; attached to wall of coelom	Lateral to gut; attached to wall of coelom	Dorsolateral to gut; unattached	Dorsolateral to gut; unattached
Filaments on eggs	Many at pole, single distant one	None	None	None
Upper beak	Pointed, short, stout; overlapped slightly by lower	Greatly produced, very fragile; slightly overlapped by lower	Moderately produced, fragile; ca. half length of lower	No beak; upper jaw broadly curved
Lower jaw (in adult)	Pointed, short, stout	Greatly produced, ca. equal to postorbital head length	Much produced, ca. twice length of upper jaw	Very short, bluntly pointed, tubercular at tip
Teeth on upper jaw	All uniserial	Biserial on beak; uniserial behind	Uniserial behind; biserial forward	Uniserial, few, widely spaced
Teeth on lower jaw	Obsolete, except developing forward only in adults; uniserial	Well developed throughout life; biserial on beak, uniserial behind	Biserial near gape; uniserial forward	Essentially uniserial, fewer anteriorly
Cartilaginous loops between mandibular rami	Few, but very well developed	Numerous over long area	Few over short area	Wholly lacking
Intermandibular tissue	Covered by upper jaw	Covered by upper jaw	Covered by upper jaw	Tissue largely exposed
Lateral line	Extending to over anal finlets	Extending to over anal finlets	To slightly past pelvic base[2]	Completely lacking
Tubes and pores of head	Numerous and much branched	Numerous and much branched	Intermediate	Few, little branched
Fiber bundles of body muscles (Figure 7)	Fine	Fine	Moderately coarse	Relatively very coarse
Caudal peduncle[3]	Short	Short	Long	Long
Procurrent caudal rays	5-7	5-7	4, rarely 3 or 5	2-3
Gill rakers[4]	37-38 (32-43)	45 [5](39-51)	22-24 (19-26)	17-18 (15-21)
Pectoral rays[4]	12-14 (12-15)	13-14 (12-15)	10-11 (10-11)	9-10 (8-11)
Vertebrae[4]	[6]65-67 (64-69); 63-67 (62-68)	65-67 (64-70)	59-62 (58-62)	56-57 (54-59)
Scales, lateral midline	128-148; rather firmly attached	107-128; rather firmly attached	77-91; very caducous	70-88; very caducous

[1]Except for gill rakers (5), characters refer to both subspecies.
[2]The lateral lines are incomplete on all our specimens except on the 121.2 mm one from Funchal, Madeira.
[3]Length of caudal peduncle, measured as interval between bases of last finlet and first precaudal ray, is either "short" (about equal to depth of peduncle) or "long" (about twice that depth).
[4]Minimum and maximum values; the most common values first with total ranges in parentheses.
[5]Values in parentheses are those for *S. s. scombroides*.
[6]First values for western Pacific, mean 66.05 (for 248 counts); second values for eastern Pacific, mean 65.11 (for 3,060 counts).

adocetus or *Nanichthys simulans*, is the basic type of the family, and that the dwarf forms are derivative.

DEVELOPMENT OF BEAK

In their early ontogeny, the Scomberesocidae, like other synentognathous fishes, pass through changes in physiognomy (Figure 2), involving especially the upper and lower beaks. The degree of metamorphosis varies greatly among the four species.

The most dwarfed scomberesocid, *E. adocetus*, exhibits the least change, retaining rather heavy, little-produced jaws throughout life. The upper jaw remains relatively short, and rounded in top view, and the lower jaw increases with growth of the fish only very slightly in production and slenderizing.

Next in degree of age changes is *C. saira*, in which the premaxillaries become more pointed forward and the dentaries become slightly produced and slenderized, but not to a degree fully warranting the designation of either jaw as a beak. In contrast with *Scomberesox* and *Nanichthys*, the snout does not further increase in relative length after the fish reaches the standard length of about 50 mm (Figure 2). In contrast, the snout increases in relative length throughout the life span of *Nanichthys* and in *Scomberesox* until a length of about 200 mm has been attained.

Next in the series we may rate the largest, and in many other respects the most extreme form, *S. saurus*. Very small juveniles have a short muzzle, with the lower jaw, as in all the species, the heavier (Figure 2). Very early the jaws both become sharper forward and begin to elongate. The process is initially somewhat more accelerated in the lower jaw, but at no stage do the developing beaks simulate the condition found in halfbeaks, for the developing upper beak is always much more than half as long as the lower. Lütken's (1880) indication to the contrary resulted from his inclusion of *N. simulans* into what he treated as the developmental series of *S. saurus* (see p. 533). In fact, the relative projection of the lower jaw decreases but little with age (Figure 2).

The most extreme ontogenetic changes in physiognomy are displayed by the next-to-most dwarfed form, *N. simulans* (Figure 2). Until it reaches about 30 mm SL the jaws are scarcely produced. Soon, however, the premaxillaries become pointed forward and begin to elongate, but slowly. The dentaries become very slender and, in juxtaposition, elongated forward far beyond the slender conjoined tips of the premaxillaries. When the standard length has reached 60 mm, the lower beak of *Nanichthys*, in contrast with *Scomberesox*, is more than twice the length of the upper. *Nanichthys* thus displays the closest approach to the halfbeak condition, but it can hardly be said to pass through a halfbeak stage, as do the belonids and two genera commonly (*Oxyporhamphus*) and/or regularly (*Fodiator*) placed in the Exocoetidae (Lütken 1880; Nichols and Breder 1928; Breder 1932, 1938; Hubbs 1933; Parin 1961). The projection of the lower jaw as a proportion of length of fish increases sharply with age, at least for the usual standard lengths of about 90 mm in the specimens available to us.

PHYLOGENY

Only two extant genera of the family Scomberesocidae, *Scomberesox* Lacépède 1803, and *Cololabis* Gill 1895, have been recognized. They have been differentiated primarily on the basis of the degree of development of the jaws into beak-like structures; in *Scomberesox* each jaw is definitely prolonged, very slender, fragile, and elongate, whereas in *Cololabis* the jaws remain short, less fragile, and only moderately pointed (Figures 1, 2). In each genus the lower jaw projects slightly beyond the upper. Both genera comprise slender, elongate fishes, bearing, as do the unrelated Scombridae, a file of separated finlets that largely fill the interval between the caudal fin and the main parts of the dorsal and anal fins. *Scomberesox* attains a standard length rarely in excess of 450 mm, although there are undocumented reports of 500 mm. *Cololabis* reaches about 350 mm SL.

Despite the several expressed opinions to the contrary (below), we regard the merely pointed muzzle, with projecting chin, as in *Cololabis* and *Elassichthys* (Figure 2), as a primitive feature, and as also in *Arrhamphus*, *Chriodorus*, and *Melapedalion* of the halfbeaks. We also regard the beaks of *Scomberesox* and *Nanichthys* as derivative therefrom. Jordan and Evermann (1896) surmised that *Cololabis* "represents the immature state of *Scomberesox*"—a view repeated by others of that school. Schlesinger (1909) definitely treated the jaws of *Cololabis* as secondarily foreshortened. Nichols and Breder (1928) went so far as to characterize *Cololabis* as ". . . a recogniz-

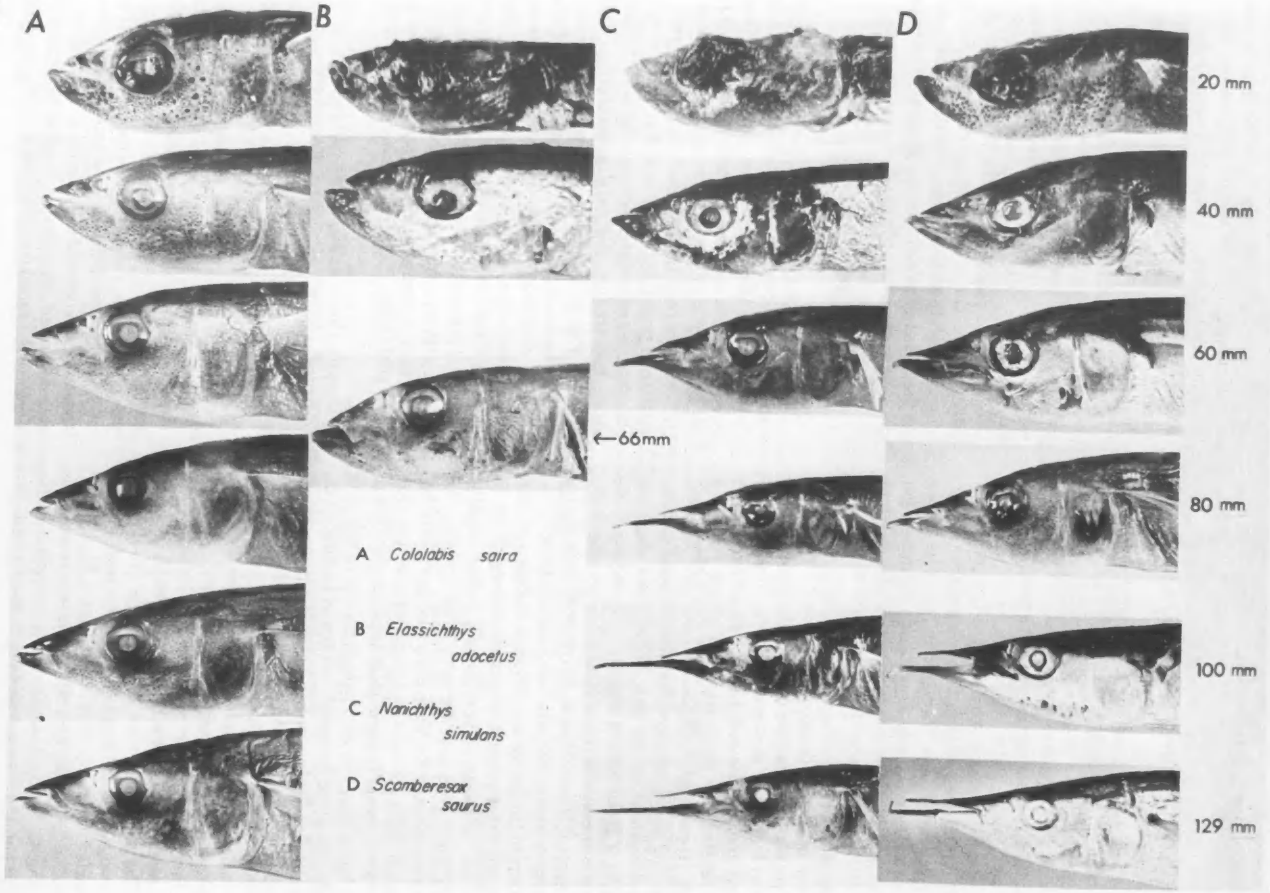

FIGURE 2.—Development of beaks in young of the four genera and species of scomberesocid fishes. Specimens are aligned in rows by size (standard length).

able fixed larva of *Scomberesox*." Knowing *C. saira* well as a moderately large and extremely active surface fish leads us to emphatically disregard its consideration as a larva. There is nothing in the ontogeny of the four species of the family to support the view that beaklessness arose from the beaked condition.

Thus, we arrive at the concept of a relatively large and strong, beakless, surface-swimming fish as the phyletically basic member of the Scomberesocidae: *Cololabis* alone fits this concept. We therefore assume that an immediate ancestor of *C. saira* gave rise to the other members of the family and remains as a relic in the temperate waters around the North Pacific, where it appears to replace *Scomberesox* completely.

The *Cololabis* ancestor presumably gave rise to *Scomberesox* through the development of a long beak, by the loss of filaments on the egg, and through a moderate increase in size and in average number of gill rakers and vertebrae. Perhaps a stock of the ancestor crossed equatorial waters in some past cool period and became isolated when the tropics again became warm; differentiation may then have taken place. From cool South Pacific waters the West Wind Drift may be assumed to have transported the saury to the southern parts of the Atlantic and Indian Oceans. From the Cape region of Africa it could have been carried far northward on the Benguela Current and may somehow, at some time, possibly even in the Pleistocene, have transgressed the tropics to gain the favorable waters of the North Atlantic. Such movements, however, are hypothetical.

The origin of the dwarfs from a type or types more like *Cololabis* and *Scomberesox* seems hardly subject to doubt (as is indicated above). While recognizing the many features, some deep-seated and fundamental, wherein *Elassichthys* and *Nanichthys* closely agree, and jointly contrast with *Cololabis* and *Scomberesox* (Table 1), we strongly favor, albeit somewhat intuitively, the hypothesis that they are the products of convergent evolution: that *Elassichthys* stemmed from *Cololabis* (or an immediate ancestor of that genus), and that *(Nanichthys* is an offshoot from *Scomberesox* (or its immediate ancestor).

Circumstances favoring the concept of a dual origin of the two dwarf species follow.

1) Characters held jointly by *Elassichthys* and *Nanichthys*, in contrast with *Cololabis* and *Scomberesox*, are of the sort that might well be related to dwarfing, and hence be susceptible to independent origin. The lack of the gas bladder seems compensated for by the greatly reduced size of the fish (yielding relatively more surface and viscosity per weight), and by the apparently weaker musculature. The single ovary may be related to the minute size of the organ and the proportionately immense size of the few ova containable at any one time. The degeneration of the lateral line is a common feature of dwarfed fishes. The great reduction in number of gill rakers would be expected, as the smaller number should give adequate straining in a space so greatly reduced. Reduced number of vertebrae and rays is a feature of dwarfing, as Te Winkel (1935) showed in her study of a neotenic goby, and as she and the senior writer showed in an unpublished study of the excessively neotenic fish genus *Schindleria* (which was originally misplaced in the Synentognathi, though it is not so related—as Gosline (1959) has shown).

2) The agreement between *Elassichthys* and *Cololabis* in the mere sharpening of the jaws (the upper rounded in *Elassichthys*), without any real beak development, is a compelling reason to regard them as closely related.

3) The circumstance that the gill rakers and vertebrae are fewer in *Cololabis* than in *Scomberesox*, and about proportionately fewer in *Elassichthys* than in *Nanichthys* is at least suggestive evidence.

4) The circumstance that *Cololabis* is somewhat smaller than *Scomberesox*, and that *Elassichthys* is proportionately smaller than *Nanichthys*, seems to provide similar confirmatory evidence.

5) The mutual occurrence of *Elassichthys* and *Cololabis* in the Pacific Ocean, in part sympatrically, and the mutual occurrence of *Nanichthys* and *Scomberesox* in the Atlantic and Indian Oceans, again in part sympatrically, provides strong confirmatory evidence that *Elassichthys* is the dwarf derivative of *Cololabis* and that *Nanichthys* stemmed similarly and independently from *Scomberesox*. This hypothesis is diagrammed in Figure 3A. On this concept, dwarfing and various structural changes (diagrammed as "d g o"), including the loss of the gas bladder and the change to a single ovary, occurred twice, whereas the evolution of a beak (marked as "b") occurred only once.

No such body of evidence seems advanceable for the alternative hypothesis (Figure 3B) that dwarfing and the ancillary changes occurred but

FIGURE 2.—Development of beaks in young of the four genera and species of scomberesocid fishes. Specimens are aligned in rows by size (standard length).

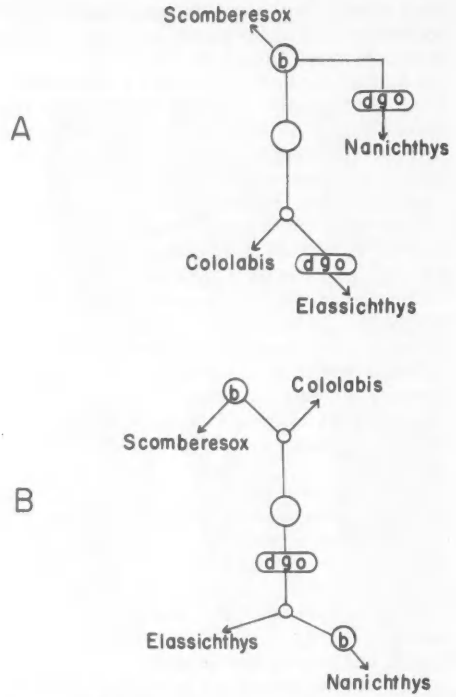

FIGURE 3.—Diagrams (A and B) of hypothetical divergent evolution within the Scomberesocidae: b—well-developed beak; d—dwarfism; g—gas bladder lost; o—ovary single. (A) The larger *Scomberesox* and the dwarfed *Nanichthys*, and the larger *Cololabis* and the dwarfed *Elassichthys*, derived respectively from beaked and beakless ancestors; development of a beak occurred but once, dwarfism and structural changes (d g o) twice. (B) The beaked and beakless larger forms, *Scomberesox* and *Cololabis*, derived from a common ancestor, as did the beaked and beakless dwarfs, *Elassichthys* and *Nanichthys*; development of a beak occurred twice, dwarfism and the structural changes but once.

once, so that *Elassichthys* and *Nanichthys* are of immediate common origin. On this hypothesis, the beak would have developed independently in *Nanichthys* and *Scomberesox*. The differences between the two genera in the lengths of the upper and lower beaks could be cited as confirmatory evidence. As another item of evidence it could be stated that agreement between *Elassichthys* and *Cololabis* breaks down when the structure of the egg is considered.

For some years we have known that there is a distinct dwarf genus (*Nanichthys*) having many characters in common with *Scomberesox*, as well as another dwarf genus (*Elassichthys*) having much in common with *Cololabis*. The species involved we name *Nanichthys simulans*, new species, and *Elassichthys adocetus* (Böhlke 1951).

These conclusions have been rather widely shared with colleagues. Parin (1968a, b) in particular, has discussed these putative relationships, using the names "*Scomberesox* sp." and "*Cololabis adocetus*" for the respective dwarfs; he cited only superficial distinctions, along with reduced numbers of gill rakers and vertebrae, in the dwarf form. Dudnik (1975b), likewise using the name "*Scomberesox* sp.," also discussed *Nanichthys*; he noted one internal morphological feature, that one of the ovaries is rudimentary. We have consistently found, however, no trace of a second ovary in either *Elassichthys* or *Nanichthys*. Our findings have been mentioned also by Collette (1966) as the second case of paedomorphism in the order, during his indication of a third case, that of a "paedomorphic or neotenic" belonid. The first case he indicated as the suggestion by Nichols and Breder (1928) that the scomberesocid genus *Cololabis* is a permanently arrested stage in the ontogenetic development of *Scomberesox*.

TABLE 2.—Numbers of gill rakers for the scomberesocid fishes.

Gill rakers	*Scomberesox saurus*		*Cololabis saira*	*Nanichthys simulans*	*Elassichthys adocetus*
	scombroides	*saurus*			
15	—	—	—	—	12
16	—	—	—	—	51
17	—	—	—	—	120
18	—	—	—	—	135
19	—	—	—	1	53
20	—	—	—	3	27
21	—	—	—	6	5
22	—	—	—	24	—
23	—	—	—	19	—
24	—	—	—	12	—
25	—	—	—	8	—
26	—	—	—	4	—
32	—	—	2	—	—
33	—	—	5	—	—
34	—	1	23	—	—
35	—	5	34	—	—
36	—	11	47	—	—
37	—	9	84	—	—
38	—	17	63	—	—
39	6	18	50	—	—
40	12	20	43	—	—
41	28	18	16	—	—
42	36	6	8	—	—
43	47	5	3	—	—
44	41	3	—	—	—
45	43	1	—	—	—
46	35	—	—	—	—
47	19	—	—	—	—
48	11	—	—	—	—
49	11	—	—	—	—
50	4	—	—	—	—
51	3	—	—	—	—
N	296	114	378	79	403
$\bar{x}$	44.11	39.19	37.53	22.84	17.66

TABLE 3.—Numbers of pectoral fin rays (both sides counted) and of total anal and dorsal fin rays (including finlets) for the scomberesocid fishes.

Fin rays	*Scomberesox saurus*[1]	*Cololabis saira*	*Nanichthys simulans*	*Elassichthys adocetus*
Pectoral:				
8	—	—	—	6
9	—	—	—	203
10	—	—	99	122
11	—	—	54	1
12	8	124	—	—
13	108	962	—	—
14	37	388	—	—
15	1	8	—	—
N	154	1,482	153	332
$\bar{x}$	13.20	13.19	10.35	9.36
Dorsal:				
14	—	3	14	31
15	6	97	49	183
16	45	422	16	136
17	28	185	—	19
18	1	15	—	6
N	80	722	79	375
$\bar{x}$	16.30	16.16	15.03	15.43
Anal:				
16	—	—	—	1
17	1	—	1	13
18	18	24	9	103
19	84	250	48	188
20	30	370	20	49
21	11	67	—	2
N	144	711	78	356
$\bar{x}$	19.22	19.68	19.11	18.78

[1]Counts for all fin rays of the northern and southern subspecies of *Scomberesox saurus* are combined.

TABLE 4.—Numbers of vertebrae for the scomberesocid fishes.

Number of vertebrae	*Scomberesox saurus*	*Cololabis saira*	*Nanichthys simulans*	*Elassichthys adocetus*
54	—	—	—	14
55	—	—	—	74
56	—	—	—	224
57	—	—	—	186
58	—	—	2	52
59	—	—	11	6
60	—	—	30	—
61	—	—	46	—
62	—	12	21	—
63	—	115	—	—
64	9	672	—	—
65	73	1,212	—	—
66	149	840	—	—
67	83	187	—	—
68	20	21	—	—
69	3	1	—	—
70	1	—	—	—
N	338	3,060	110	556
$\bar{x}$	66.13	65.14	60.66	56.37

[1]Counts for the southern and northern subspecies are combined.

The much reduced size of *Nanichthys* and the even more extreme dwarfing of *Elassichthys* strongly support the hypothesis that they exhibit neotenic or paedomorphic tendencies, certainly dwarfism; we hold that they are not neotenic, in the strict sense, but merely dwarfed. The reduced numbers of gill rakers, pectoral rays, vertebrae (Tables 2-5), scales, and procurrent caudal rays provide confirmatory evidence (no marked differences were found in the numbers of dorsal and anal rays, either in the main fin or in the finlets). The loss of one ovary (or the complete fusion of the pair), and a tremendous decrease in the production of ova, the more notable in *Elassichthys*, may well be correlated with the dwarfing of the two new genera (the ova, however, have not been notably decreased in size). The less extreme dwarfing of *Nanichthys* could be interpreted as reflecting the larger size of its presumed progenitor, *Scomberesox* (Figure 1, Table 1). The concept of *Nanichthys* and *Elassichthys* being the respective derivatives of *Scomberesox* and *Cololabis* could be interpreted as being supported by their similar beak structures (Figure 2), and by the common occurrence of *Scomberesox* and *Nanichthys* in the Atlantic and Indian Oceans and of *Cololabis* and *Elassichthys* in the Pacific, north of the range in that ocean of *Scomberesox*.

Herein we describe, discuss, and differentiate the two new dwarfed genera, *Nanichthys* and *Elassichthys*, and the new species *N. simulans*, distinguish the Southern Hemisphere population of *Scomberesox* as a subspecies, for which the

TABLE 5.—Correlated counts of precaudal and caudal vertebrae of the four genera of Scomberesocidae. Counts not otherwise marked represent *Elassichthys*; counts in italics refer to *Nanichthys*; counts in parentheses represent *Cololabis*; and counts in bold face type refer to *Scomberesox*.

Genus	Precaudal vertebrae	Caudal vertebrae								
		21	22	23	24	25	26	27	28	29
Elassichthys	32	—	1	1	1	—	—	—	—	—
	33	2	7	23	8	—	—	—	—	—
	34	1	21	52	8	—	—	—	—	—
Nanichthys	35	—	7	5	1 2		1	—	—	—
	36	—	—	1 4	*21*	*14*	2	—	—	—
Cololabis	37	—	*1*	7	*41*	22	(7)	(8)	(6)	—
	38		*1*		*7*	3	(37)	(64)	(21)	(1)
Scomberesox[1]	39	—	—	—	—	(3) 1	(37)	(63) 1	(10)	(1)
	40	—	—	—	—	**12**	**13** (11)	(15)	(4)	—
	41	—	—	—	**17**	**63**	**31**	**1**	—	—
	42	—	—	—	**6**	**19**	**6**	**1**	**1**	—
	43	—	—	—	**2**	**2**	—	—	—	—

[1]Counts for the southern and northern subspecies are combined.

name *S. saurus scombroides* (Richardson 1842) appears to have priority, and we portray the zoogeography of the four genera of the Scomberesocidae that we now recognize. Also, we append a discussion of Miocene fossils from California referred to the Scomberesocidae.

MATERIALS AND METHODS

We have examined material from the following repositories: AMS (Australian Musuem, Sydney); BCFL (Bureau of Commercial Fisheries Laboratories (now NMFS), at Brunswick, Ga.; Honolulu Hawaii (formerly POFI); Seattle, Wash.; and Woods Hole, Mass.); BMNH (British Museum (Natural History)); BU (Boston University); CAS (California Academy of Sciences); CF (Carlsberg Foundation); CFG (California Fish and Game, San Pedro); CNHM, FMNH (Chicago Natural History Museum, Field Museum of Natural History); LACM (Los Angeles County Museum); MCZ (Museum of Comparative Zoology, Harvard University); MMF (Museo Municipal do Funchal, Madeira); SAM (South African Museum, Cape Town); SIO (Scripps Institution of Oceanography); SOSC (Smithsonian Oceanographic Sorting Center); SU (Stanford University; collections now at CAS); TABL (Tropical Atlantic Biological Laboratory, Miami); UMMZ (University of Michigan Museum of Zoology); USNM (United States National Museum); UW (University of Washington, Seattle); WHOI (Woods Hole Oceanographic Institution); ZMUC (Zoological Museum, University of Copenhagen); and ZSZM (Zoologisches Staatsinstitute und Zoologisches Museum, Hamburg).

Counts of dorsal and anal rays include the succeeding finlets because the last rays of the main fin proper are often too much like those of the first finlets for definitive separation, particularly in adults; usually the last rays of the fin proper are thickened at the base and much branched and fanlike distally—in shape much like that of the first finlet. In young and subadults a space greater than that between the last rays of the fin proper usually separates the last ray and the first finlet, but this space is often obscured by a membrane or is not apparent in large specimens, particularly of *Scomberesox* and *Cololabis*. Pectoral rays of small and juvenile fish were counted using an air jet, or when submerged. Vertebrae were counted from radiographs or stained material (the latter method was used primarily for juveniles of *Cololabis*). The urostyle was included in the count.

Numbers of gill rakers for specimens of *Scomberesox* and *Cololabis* <70 mm SL and of *Nanichthys* and *Elassichthys* <30 mm SL are not included in the tabular data because at shorter sizes the anterior rakers fade gradually into diminishing nubs of tissue that require highly subjective interpretation.

Lateral lines scales were removed from the left side within a distance no >10 mm anterior to the origin of the pelvic fin. To enhance visibility of circuli the scales were lightly stained in a weak solution of Alizarin Red S and visually monitored for adequate uptake of stain. The scales of both *Scomberesox* (particularly) and of *Cololabis* were quite tenacious, so much so that they needed to be cut away from the body and the adhering tissue manually removed. Remaining bits of tissue often were so firmly attached that they could not be pulled off with forceps; immersion in 2% KOH eroded the scales without removing the bits of tissue.

As most specimens of *Scomberesox* examined had the tips of the beaks broken off, proportions in all the species are based on body length rather than standard length. Body length is defined as the distance from the posterior margin of the orbit to the end of the hypural plate; this end point was determined by flexing the caudal fin until a crease appeared, approximately at the end of the hypural.

KEY TO SPECIES OF SCOMBERESOCID FISHES

1a. Gill rakers numerous (34-51), very closely spaced. Pectoral rays 12-15. Procurrent caudal rays 5-7. Depth of caudal peduncle equal to or less than its length 2

1b. Gill rakers fewer (15-26), less closely spaced. Pectoral rays 8-11. Procurrent caudal rays 2-5. Depth of caudal peduncle one-half to less than its length 3

2a. Both jaws produced into long, slender beaks in specimens >100 mm SL, the lower slightly longer. Maximum size about 450-500 mm SL. Known from temperate waters of North Atlantic and all southern oceans ..... *Scomberesox saurus*

2b. Jaws only moderately produced into blunt beaks, the lower slightly longer. Maximum size about 400 mm SL. Native only in North Pacific Ocean ..... *Cololabis saira*

3a. Jaws of adults produced as slender beaks, the lower about twice the length of upper. Gill rakers 22-24 (19-26). Procurrent caudal rays 4 (3-5). Maximum size to 126 mm, usually about 100 mm. Known only from warm-temperate waters of Atlantic and Indian Oceans ..... *Nanichthys simulans*

3b. Upper jaw very little produced, bluntly rounded, the lower jaw slightly more produced and more pointed at all sizes. Gill rakers 17-18 (15-21). Procurrent caudal rays 2-3. Maximum size to 68 mm SL. Known only from eastern tropical Pacific and westward to Hawaii ..... *Elassichthys adocetus*

AIDS TO IDENTIFICATION

If the specimen is determined to be one of the larger species, pertinence to *S. saurus* or *C. saira* will be obvious from the oceanic source of the material, and, for all but the very young, from the presence or absence of a beak (Figure 2); even if the long beaks of *Scomberesox* are broken off near the base the stubbed condition will be obvious. However, if the very young of one or both species should be taken in the eastern Pacific Ocean in the upwelling area along the Equator (which now seems unlikely from the distributional evidence discussed below), it would hardly be feasible to arrive at a certain identification on the basis of beak development alone until the beak begins to develop at about 40 mm SL; but the reduced numbers of pectoral and procurrent caudal rays and of gill rakers (rather short and widely spaced) readily distinguish *Elassichthys* from *Scomberesox* and *Cololabis*. The development of the beak is the most trenchant distinction between *Scomberesox* and *Cololabis*; counts (Tables 2-5) and morphometric values (Table 6) overlap widely.

If the specimen is determined to be a dwarf, its pertinence to *E. adocetus* or *N. simulans* will probably always be determineable from the locality of capture, and, for specimens longer than about 50 mm, from the incipient to full development of the beak (Figure 2); in fact, in *Elassichthys* the upper jaw never becomes really beaklike, only broadly rounded, not moderately pointed as in *C. saira* of comparable size (Figure 4). If further check is desired, separations may be attained by counting gill rakers, pectoral rays, or vertebrae (Tables 2-5). Ueyanagi and Doi (1971) showed that in young of *Elassichthys* (≤30 mm) the depth of the caudal peduncle was one-half or less of its length, but was about equal in *S. saurus* and *C. saira*. We find (original data) *N. simulans* to have a ratio of depth to length of caudal peduncle similar to that of *E. adocetus*. These ratios hold for all sizes of the four species.

The scomberesocid fishes inhabiting the Atlantic or Indian Oceans may be either *N. simulans* or *S. saurus*, determinable by the meristic counts (Tables 2-4). At lengths greater than about 60 mm, the relative development of unbroken beaks should ordinarily be decisive (Figure 2).

TABLE 6.—Selected body proportions from 36 specimens each of the four species of scomberesocid fishes (thousandths of body length).

	Scomberesox saurus saurus (26-223 mm)		*Scomberesox s. scombroides* (63-300 mm)		*Nanichthys simulans* (32-77 mm)		*Elassichthys adocetus* (29-60 mm)		*Cololabis saira* (50-239 mm)	
Body proportion	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Orbit length	49	36-39	45	37-59	52	41-64	50	43-58	43	35-53
Postorbital head length	104	82-124	105	92-120	99	88-111	89	80-102	113	103-126
Body depth at origin of pelvic fin	132	109-160	128	115-139	113	95-135	115	95-131	136	121-153
Distance from origins of dorsal and anal fins	127	105-143	123	111-137	108	98-119	107	93-116	127	111-147
Posterior margin of orbit to origins of:										
Pelvic fin	513	474-525	501	475-536	460	444-487	447	417-485	478	457-502
Anal fin	661	611-692	669	642-707	621	604-645	628	606-654	643	620-668
Dorsal fin	684	650-715	685	658-723	648	631-672	652	630-673	679	661-707
End of hypural to origins of:										
Pelvic fin	512	487-538	515	483-542	549	529-565	560	529-586	529	518-546
Anal fin	354	317-396	343	314-371	388	363-406	380	351-400	361	326-381
Dorsal fin	330	298-369	322	281-350	359	341-379	357	330-374	329	312-350

FIGURE 4.—Upper—Dorsal view of bluntly rounded tip of upper beak of adult *Elassichthys adocetus*, 59.0 mm SL. Lower—Dorsal view of moderately pointed tip of upper beak of juvenile *Cololabis saira*, 58.0 mm SL.

DESCRIPTION OF NEW TAXA

Nanichthys Hubbs and Wisner, new genus

New genus, Hubbs and Wisner.—Collette 1966:4, 6, 7, 20 (reduced counts; neotenic [this seems to be the only published reference to *Nanichthys* as a genus]).
Genotype, *Nanichthys simulans*, new species.

Diagnosis.—A dwarfed scomberesocid (maximum known standard length 126 mm), agreeing with *Elassichthys* in having a single median ovary, when ripe largely filling the expanded coelom, and the testis folded together into a single median band. Gas bladder completely obsolete. Lateral line developed only anteriorly. Premaxillary and mandibular tooth rows closely approximated at front. Upper jaw produced as an extremely slender beak about half as long as in *S. saurus* and much slenderer (in both lateral and dorsal aspects) than the much stronger but still slender lower beak, which is only about half as long as, and much less attenuate than, that in adult *S. saurus*. The major

counts are much reduced: vertebrae 58-62, transverse scale rows along midlateral line 70-88, procurrent caudal rays 4 (rarely 3 or 5), pectoral rays 8-11, rakers on first gill arch 19-25 (usually 22-24).

Derivation of generic name.—From the Greek νᾶνοσ (nanos), a dwarf, and ιχθῦσ (ichthys) a fish.

Nanichthys simulans Hubbs and Wisner, new species Figure 5

Derivation of species name.—From the Latin, *simulans* (imitating).

Holotype.—SIO 63-546, an adult male 89.5 mm SL, dipnetted at surface under a light in the south central Atlantic Ocean at 24°02.5′ S, 15°32.0′ W, on 9 June 1963; deposited in the Marine Vertebrate Collection of the Scripps Institution of Oceanography.

Paratypes.—All dipnetted in the southern Atlantic Ocean at night under a light. Marine Vertebrate Collection of the Scripps Institution of Oceanography: SIO 63-545, 8 (46-69 mm), 12 June 1963, 29°51.5′ S, 11°07′ W; SIO 63-546, 17 (47-90 mm), 19 June 1963, 24°02.5′ S, 15°32.0′ W; SIO 63-548, 16 (20-76 mm), 20 June 1963, 23°42.0′ S, 12°12.5′ W; SIO 63-549, 6 (55-87 mm), 22 June 1963, 21°21.0′ S, 11°34.5′ W; SIO 63-550, 7 (45-80 mm), 24 June 1963, 20°10.5′ S, 11°30.5′ W; SIO 63-553, 4 (67-90 mm), 26 June 1963, 17°39.0′ S, 12°22.0′ W; SIO 63-555, 11 (38-66 mm), 28 June 1963, 15°48.0′ S, 16°50.0′ W; SIO 63-571, 2 (38 and 44 mm), 22 July 1963, 11°35.0′ S, 44°01.0′ W.

USNM 204257, 2 (68 and 101 mm), 15°45′ S, 08°45′ E; USNM 204258, 4 (42-66 mm), 32°57′ N, 39°21′ W.

We plan to transfer some of the Scripps paratypes listed above to USNM, MCZ, Philadelphia Academy of Natural Sciences (ANSP), CAS, and BMNH.

We do not assign paratype designation to many additional specimens, mostly very small, from the mid-Atlantic, nor to the few examples seen from the Indian Ocean, nor to two specimens, unusually large for this dwarf species, from Funchal, Madeira (these two are discussed on p. 541).

Synonymy of *Nanichthys simulans*

Scombresox scutellatus (not *Scomberesox scutul-*

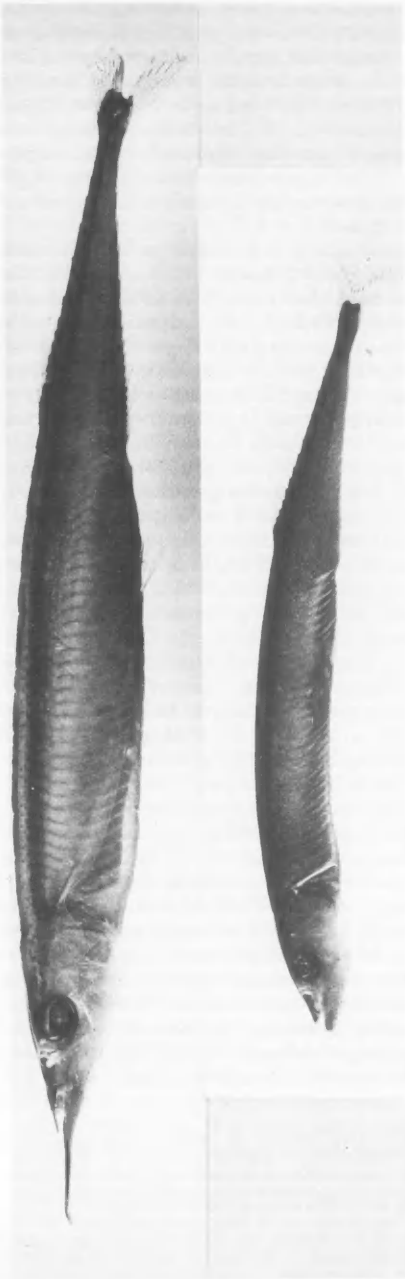

FIGURE 5.—Upper—*Nanichthys simulans*, holotype, adult male, 89.5 mm SL, SIO63-546. Lower—*Elassichthys adocetus*, adult male, 64.7 mm SL, SIOH52-380.

latum LeSueur 1822:132-133[2])—Valenciennes 1846:477-479 (description: "en le retirant de l'estomac d'un coryphène (*Coryphaena equisetis*) . . . venait de pecher à vingt-cinq lieues [ca. 2.76 mi] au nord de Sainte-Hélène [St. Helena Isle, about 16° S in mid-Atlantic Ocean]; nous avons un second exemplaire de la même espéce . . . fit à l'Isle-de-France [Mauritius Island, Indian Ocean] ou pendant sa traversée de retour" [to France].

Scombresox saurus (misidentification).—Günther 1866:257-258 ("Atlantic, 3° N of the line"; St. Helena; probably also 20° N, 22°53′ N and other series); 1889:34 (". . . fry and young . . . belong to most common forms of pelagic life . . . from the Atlantic . . . .").[3] Sauvage 1891:526 (listed from near Madagascar, between 3° and 26° S, 42° and 65° E; presumed from locality). Murray and Hjort 1912:89, 90, 94, 607, 613 (14 stations listed), 633, 635, 644, 670, 741, 747-748, figs. 541-542, all in part or questionable, listed both as "*Scombresox*" and as "*Scombresox saurus*," from open Atlantic in area between Iceland, Morocco, and Newfoundland; size to 50 cm. Barnard 1925:259, fig. 16b (St. Helena record only). Cadenat 1950:298 (presumed from locality off Iles du Cap Vert).

Scomberesox saurus (misidentification).—Lütken 1880:564-569, 1 fig., repeated by Murray and Hjort, see above (in part: in Atlantic Ocean from 11°30′ to 48° N, 9° to 40° W, and from 12° to 40°32′ S, 52° W to 16°30′ E; in Indian Ocean from 27° to 38°20′ S, and from 24°30′ to 101°40′ E; measurements and counts presumably also in part). Regan 1916:142 (postlarvae from south of Azores, at 29°10′ N, 33°36′ W, identification dubious). Bigelow and Welsh 1925:166, fig. 71 (range, 11°-12° to 40° N in Atlantic (presumably in part), figure repeated from Murray and Hjort, see above). Hildebrand and Schroeder 1928:151-152 (range, in part, and description of young, from Bigelow and Welsh 1925). Sivertsen 1945:6 (in part, St. Helena record only). Bigelow and Schroeder 1953:170-171, fig. 83 (in part, doubtful, description; young—100 to 150 mm "hemiramphus stage," most numerous in open Atlantic between 11° or 12° and 40° N). Smith 1955:308 (presumptive, listed from Aldabra Island). Fowler 1956:141-142 (reference to Borodin's 1930 dubious (unverified) Red Sea record; South Africa, description taken from New England and New York material of *S. saurus* and not "Indo-Pacific" entry). Briggs 1958:264 (presumptive, in part, western Atlantic from Newfoundland and Bermuda to Argentina, 35° to 30° S). Rodríguez-Roda 1960:115 (presumed from locality; southern Spain, Strait of Gibralter). Hotta 1964:4-5 (in part, presumptive, distribution). Leim and Scott 1966:168 (in part, presumptive, in western Atlantic south to West Indies; fry abundant between 11° and 40° N; jaws do not reach full length until fish are 4 to 6 in long). Sauskan and Semenov 1969:250-252, fig. 157 (two populations inferred in North Atlantic, 32° to 36° N, 50° to 70° W, and near Azores; feeding migration) (in part, presumed from locality). Zilanov and Bogdanov 1969, fig. 158 (size groups, migrations, northeast Atlantic, 30° to 60° N, 8° to 40° W) (in part, presumed from locality). Hartmann 1970 (2.0 mm eggs in 68 mm scomberesocids from northeastern Atlantic can refer to only *N. simulans*).

Scomberesox sp.—Parin 1968b, fig. 31 (planktonic, records mapped in tropical eastern Atlantic and north of Madagascar, Indian Ocean); 1968a, fig. 1 (undescribed species under study by Hubbs and Wisner). Parin and Andriashev 1972 (dwarf Atlantic species, along 26° W between 24° and 30° S, and in western cruise track off South America in area of 32° S, temperature 20.4° to 22.4° C). Parin 1973 (reference to Parin 1968a; to be described by Hubbs and Wisner; abundant, epipelagic, Atlantic off Madeira, Canaries, Morocco, Portugal, to 40° N). Ueyanagi et al. 1972, fig. 1, 2 (sizes graphed, distribution in Atlantic mapped). Suda 1973, fig. 7 (life history presumably similar to that of *Cololabis adocetus;* not suitable for commercial fishery). Dudnik 1975b, fig. (general discussion; comparison with *S. saurus* in range and characters; one ovary developed, second rudimentary; ova sizes; spawning prolonged). Wisner 1977, fig. (description, key; compared with *S. saurus*, Belonidae, and Hemiramphidae; distribution in northwestern central Atlantic). Hardy 1978, fig. 29-34 (in part, North Atlantic: "*Scomberesox* sp." in reference to Hartmann, 1970, statement of 2.0 mm eggs in females 68 mm and over).

[2]LeSeuer's type-specimen was "small," with upper beak about half of other; it was ". . . found in the stomach of a fresh codfish which had been brought to Boston from the Bank of Newfoundland," therefore in the appropriate range of *Scomberesox saurus* and far north of the range of *Nanichthys simulans*.

[3]At least in part; one of three specimens involved, but not mentioned, from Tenerife (one of the Canary Islands) has been identified for us as *N. simulans* by G. Palmer of the British Museum (Natural History), using characters outlined by us.

Discussion of Synonymy.—It has been consistently overlooked that Valenciennes [1846 (XVIII):477-479] recognizably described this dwarf scomberesocid, from 25 leagues north of Saint Helena Island in the tropical Atlantic Ocean and from Mauritius Island in the Indian Ocean or on the return journey [to France]. He misidentified this species as *Scombresox scutellatum* LeSeuer. However, *Scombresox scutellatum* LeSueur (1822) was based on a small specimen, obviously of *Scomberesox saurus*, that was taken from the stomach of a cod brought to Boston from the bank of Newfoundland. The Atlantic specimen described by Valenciennes also was supposed to be a young saury that had been eaten by a dolphin fish, identified as *Coryphaena equisetis*, caught "à vingt-cinq lieues au nord de Sainte-Hélène." Assuming this to be the island on which Napoleon was confined, on the basis of 2.76 mi to a league, from the old French system, the location was approximately 14°48′ S, 05°42′ W (marked as an open circle on Figure 12). This location is obviously within the now known habitat of *Nanichthys simulans* and far from the range of *S. saurus*, whereas the specimen treated by LeSueur was centered within the area where *S. saurus* alone occurs, in abundance.

That Valenciennes had an example of the dwarf Atlantic saury is obvious from his description of the beak in a small specimen. Valenciennes wrote: "La brèvité du museau est aussi non moins remarquable; car le longueur du bec n'est quère moitié du reste de la tete; le bec supérieur lui-meme n'est pas beaucoup plus prolongé que celui des plusieurs hémiramphes." He further stated (p. 478), "Ce petit poisson, long de deux pouces neuf lignes. . . ." Since the old French "pouce" was 27.07 mm long, and a "ligne" one-twelfth of a pouce, we compute the length of the fish as about 75 mm. A scomberesocid of this size, with beak scarcely half the length of the head behind the beak, and with snout comparable with that of a hemiramphid, could scarcely be other than a *Nanichthys*. Since the specimen collected at "l'Isle-de-France" [Mauritius], or on the return journey, was described as of the same size and of the same species, and since *N. simulans* is now known to occur in the southern Indian Ocean, it has seemed highly probable that it also pertains to that species. This assumption has been verified for us, very kindly, by Marie-Louise Bauchot[4] who has found that the two specimens, respectively 66.9 and 67.1 mm SL, have 11 and 10 pectoral rays, 23 and 22 gill rakers, and 59 and 60 vertebrae (within the range for *N. simulans* but far below the range for *S. saurus*).

It is now clear that Lütken (1880:564-569, fig. a-h) unknowingly included *N. simulans* as well as *Scomberesox s. saurus* in his account of *S. saurus*. This is evident from his statement of latitudinal distribution in the Atlantic Ocean from 11°30′ to 48° N and from 12° to 40°32′ S, and in the Indian Ocean from 27° to 38°20′ S, as well as from his figures; figures c, d, and e represent fish 51, 60, and 100 mm TL from tip of mandible to caudal-fin fork (corresponding to standard lengths of about 47, 55, and 89 mm, from tip of upper jaw to base of caudal fin). Beaks of specimens f-h (170 mm to full adult) pertain to *Scomberesox*. Comparison of these three figures with our illustrations of growth changes in the four species (Figure 2) demonstrates agreement only with *N. simulans*. The divergent approach toward hemiramphine beak structure in this developmental series of *Nanichthys* apparently did not disturb Lütken, for he showed in the same compilation of figures the development of *Belone vulgaris* from the beakless very young through the halfbeaked juveniles to the nearly full-beaked adult stage. In the lack of locality data it is not clear which species are represented by Lütken's figures a and b, which represent prejuveniles, 16 and 30 mm in fork length, with almost no beak development.

The epochal treatise of Atlantic epipelagic fishes by Murray and Hjort (1912), expanding that of Lütken (1880), recognized the preponderance of Scomberesocidae in the mid-Atlantic but failed to distinguish between *S. saurus* and *N. simulans*. Evidence in these classics, however, renders it clear that both accounts dealt with both species. Murray and Hjort's figure 541 of a 6.2 cm saury (on p. 747) almost surely represents *N. simulans* by reason of the better development of the beaks at that size (although the body was drawn too deep). Their figure 542 is a copy of Lütken's figure 567 (discussed above). The well-filamented egg labeled "Egg of Scomberesocid" (fig. 531) was obviously misidentified and very probably represents an exocoetid (Orton 1964). The treatment of sauries by Murray and Hjort pertains almost wholly to young (the maximum size given, 50 cm, was presumably drawn from some other source); they

[4]Marie-Louise Bauchot, Fish Division, Museum National d'Historia Naturelle, Rue Cuvier, 57, Paris, France, pers. commun. 2 May 1968.

stated that only "young scomberesocids" were taken on the cruise.

The accounts of *S. saurus* by Bigelow and Welsh (1925) and by Bigelow and Schroeder (1953) definitely also involved *N. simulans*. The figure of the young, after Murray and Hjort, definitely represents the dwarf species, as does the text account of the "young": "The most interesting phase in the development of the skipper is that its jaws do not commence to elongate until the fry have grown to about 1⅝ inches (40 mm.), and that the lower jaw out-strips the upper at first, so that fry of 4 to 6 (100 to 150 mm.) inches look more like little halfbeaks ('Hemiramphus' stage) than like their own parents" (quoted from Bigelow and Schroeder). These confusions were also expressed by Hildebrand and Schroeder (1928).

Inclusion of *Scomberesox s. saurus* (Günther 1889) in part, in the synonymy of this species, and the inclusion of this species in the British Museum collection, have been verified for us by G. Palmer[5] by examination, with our findings at hand, of the following specimens: six young, 31-61 mm, from St. Helena; three, 64-68 mm, from "Atlantic" (Godfrey); three, 29-93 mm, collected by Jones; one of 96 mm of the two without locality collected by Haslar; one of 69 mm taken by Vallentin at 18°32′ N, 29°09′ W; one of 52 mm, with two of *S. s. saurus*, taken at Tenerife (Canary Islands) by the *Challenger*; and one of 131 mm (total body length—see p. 541) by G. Maul in Funchal Harbor, Madeira. Günther (1866, vol. 6:257) reported *Scomberesox saurus* "From 1½ to 7 inches long" from "Atlantic, 3° N. of the line," which, on distributional grounds, assuming correct latitude, would be expected to be *Nanichthys*. However, G. Palmer reports an extant specimen 156 mm long, listed with three of 66-98 mm, from "Atlantic (Godfrey)" that is probably the 7-in specimen, but Palmer finds it to be *Scomberesox*.

Zoogeographical considerations might lead to the citation in the synonymy of *Nanichthys simulans* of the material recorded as *Scomberesox saurus* by Arnoult et al. (1966) from off Liberia and Equatorial Guinea [Iles Principe], but Marie-Louise Bauchot (see footnote 4) has informed us that a reexamination of the five specimens involved led her to reidentify them as *Strongylura senegalensis* (Valenciennes) and *Platybelone argalus* (LeSueur).

[5]G. Palmer, Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7, England, pers. commun. 3 May 1968.

Although Valenciennes (1846) applied the name *Scomberesox scutullatus* to what now seems surely to be *Nanichthys simulans* (q.v.), we regard the original *Scomberesox scutullatum* LeSueur as having been based on *S. s. saurus*. The locality "Bank of Newfoundland" is in the range of that form and probably far outside the range of its dwarfed relative. The one pertinent key character given, that of 13 pectoral rays, confirms pertinence to *Scomberesox*.

Elassichthys Hubbs and Wisner, new genus

New genus, Hubbs and Wisner.—Collette 1966:4, 6, 7, 15, 20 (reduced meristics; neotenic [this seems to be the only published reference to *Elassichthys* as a genus]).
Genotype, *Cololabis adocetus* Böhlke 1951.

Diagnosis.—A greatly dwarfed scomberesocid (maximum known standard length ca. 68 mm), agreeing with *Nanichthys* in having a single median ovary largely filling, when ripe, the expanded coelom, and the paired testes folded together into a single median band with the division on the right side. Gas bladder and lateral line scales obsolete. Upper jaw very broadly and evenly rounded in dorsal aspect and only moderately pointed in lateral view; lower jaw only moderately pointed at the tuberculate tip (Figure 4). Premaxillary and mandibular tooth rows very broadly separated at front. Counts minimal for the family: vertebrae 52-59, usually only 56 or 57; transverse scale rows along midlateral line 70-78; procurrent caudal rays reduced to only 2 or 3; rakers on first gill arch 15-21, usually 17 or 18.

Derivation.—From the Greek, ἐλάσσωνν, smaller, less, and ιχθύσ, a fish.

Elassichthys adocetus Böhlke 1951 Figure 5B

Scombresox sp.—Kendall and Radcliffe 1912:84, 167 (in part).[6]

[6]Young of *Scomberesox saurus scombroides* may well have been included; only three specimens (in Museum of Comparative Zoology), among those listed, have been examined by us and all were found to be *E. adocetus* from *Albatross* stations 4657 (07°12′30″ S, 84°09′ W), 4708 (11°40′ S, 96°55′ W), and 4730 (17°19′ S, 100°52′30″ W). *Scomberesox s. scombroides* also occurs in these areas.

Cololabis saira (misidentification).—Schaefer and Reintjes 1950:164 (between California and Hawaii at 28°22′ N, 137°12′ W; 25°14′ N, 144°41′ W; 23°52′ N, 148°41′ W; 23°04′ N, 153°19′ W; compared with "*Cololabis adocetus*," these records thought [erroneously] to confirm reference of *Cololabis brevirostris* to *C. saira* by Hubbs 1916:157 and by Schultz 1940:270). Ramírez Hernándes and Gonzáles Pagés 1976:74 (reference to Perú only).

Cololabis sp.—Clemens 1955:165 (3°31′ S, 81°11′ W [presumptive identification due to locality]). King and Iversen 1962:301, tables 19-20, appendix table 8 (one 86 mm specimen taken in Equatorial Counter Current) [identification presumed from locality].[7]

Scomberesocidae.—Mais and Jow 1960:131 (02°54′ S, 99°37′ W) [identification presumed from locality].

Cololabis adocetus.—Böhlke 1951:83-87 (original description; comparison, phylogeny; from 160 mi southwest of San Juan, Perú (17° S, 76°50′ W) (holotype); and off Perú at 10°01′ S, 80°05′ W; west of Chincha Isles, Perú, 13°35′ S, 76°50′ W; arrested development). Knauss 1957:236 (in oceanic front at about 3° N, 120° W). Gosline 1959:73 (neotenic); Gosline and Brock 1960:128, 318 (Hawaii; compared with *C. saira*). Chyung 1961:277 (reference to Böhlke 1951). Koepcke 1962:197 (references; known only from Perú, 10° to 17° S). Clemens and Nowell 1963:251-255 (records off Ecuador, Perú, Chile). Hotta 1964:4, fig. 22 (distribution off Perú). Orton 1964:144-145, 148-149 (description of pelagic and ovarian eggs from off Perú, 8°07′ to 10°51′ W; range overlaps that of *S. saurus*; vertebral numbers). Lindberg and Legeza 1965:209 translation, 1969:201 (Perú). Collette 1966:3, 15 (neoteny; meristic reduction; phylogeny; generic status). Ebeling 1967:599 (distribution mainly in central water mass in eastern Pacific Ocean). Parin 1967b:150 (117 in translation) (larvae may be caught near surface at any time of day); 1967a: many pages (distribution in very warm water). Rass 1967:58, 60, 63-66, 129 (distribution). Parin 1968b:many pages (an epipelagic fish said to be limited to tropical waters of eastern Pacific and near Hawaii); 1968a: many pages, fig. 2, 3, 5 (comparisons, relationships; distribution and ecology). Chirichigno F. 1969:40 (vernaculars in Perú, Chile). Parin 1969a:715, 719, fig. (epipelagial; distribution, dwarf fish, false pike; eastern tropical Pacific); 1969b:577 (462 in translation), fig. 2 (northern part of area surveyed off west side of South America; numerical abundance charted; as many as 1,000 trawled in 20 min with pleuston net south of Galápagos Islands). Ueyanagi et al. 1969:6-7, fig. 12 (occurrence off Perú). Ueyanagi and Doi 1971:17-21, fig. 15 (distribution in southeastern Pacific mapped; characters distinguishing juveniles of *C. adocetus* from *C. saira* and *S. saurus*). Ahlstrom 1972:1192, 1196, fig. 14 (occurrence of larvae in eastern tropical Pacific). Suda 1973:2134-2135, fig. 7 (range in eastern Pacific; dwarf species; not suitable for a commercial fishery). Chirichigno F. 1974:318-319, 331, fig. 628 (characters in key; Perú, 10° to 12° S). Nelson 1976:172 (neotenic). Parin 1975:314-316 (records near Equator at about 97° W).

The Southern Subspecies of *Scomberesox saurus*

We have found that the disjunct, widespread, circumglobal Southern Hemisphere population of *Scomberesox saurus* is slightly differentiated from the topotypic Northern Hemisphere Atlantic form, as Parin (1968a) has tentatively suggested. Before presenting the evidence we list, with annotations, the rather complicated synonymic references that apply distinctively to the southern form, and here eliminate references in which the names used are synonyms of the North Atlantic subspecies *Scomberesox saurus saurus*, namely *Scombresox*, *Scomberesox*, or *Scombresose*, *equirostrum* or *aequirostrum*, *Scombresox* or *Scomberesox rondeletii*, or *Scomberesox storeri*. We have, however, retained carded citations to those references.

Scomberesox saurus scombroides (Richardson 1842)[8]

Esox saurus.—Schneider *in* Bloch and Schneider 1801:394 (in part; "J. R. Forster MSS. II. 63"; New Zealand).

[7]The general area of the Equatorial Countercurrent, in which the small specimen was taken, is stated as between about 05° and 10° S (fig. 12). No coordinates were given for the capture but the area sampled within this current extended from about 108° to 160° W (fig. 4).

[8]The synonymy of what we treat as the Southern Hemisphere subspecies of *Scomberesox saurus* lists in sequence of first usage the varied names that have been applied thereto, whether originally based on the Northern Hemisphere form or on Southern Hemisphere material.

Scombresox saurus.—Günther 1866, vol. 6:257 (in part; records from Cape of Good Hope only). McCoy 1888:135, fig. 2 (description; Queensland). Jordan and Evermann 1896:726 (in part; reference for *S. forsteri* only). Gilchrist 1901:152 (occurrence off South Africa). Miranda-Ribeiro 1915:22 (reference to C. Berg's original account of the species in South America); 1918:16 (characters and range, in part; Montevidéo; no Brazil locality included). Barnard 1925:259-260, fig. 16 (in part; references; characters; St. Helena Bay, Table Bay, and Cape Point to Mossel Bay, South Africa; New Zealand; Australia; synonymy; general remarks). Ehrenbaum 1936:75 (Pacific and Indian Oceans only). Barnard 1950:72 (characters; St. Helena Bay to Mossel Bay in South Africa, southern Australia, and New Zealand; large schools near surface; leaping; prey).

Scomberesox saurus.—Berg 1895:25 (in part; Montevidéo). Schreiner and Miranda-Ribeiro 1902:37 (in part; habitat: Atlantic from coast of North America to Montevidéo (Berg), Africa and Europe). Gilchrist 1904:145-147, 152, pl. 10 (eggs and larvae; off Cape Point, South Africa). Devincenzi 1924:190 (reference to Berg; counts; apparently rare in Uruguay). Devincenzi and Baratini 1928:152, pl. 18, fig. 4, 5 (Uruguay). Hildebrand and Schroeder 1928:152 (in part; New Zealand). Pozzi and Bordalé 1935:159 (35°30′ S to Argentina, habitat). Fowler 1936:436-438, fig. 216 (in part; synonymy; description based on North Atlantic material; South Africa record from Barnard 1925); 1942a (Brazil)[9]. Sivertsen 1945:6 (in part; description; from stomach of *Diomedia*; North Atlantic; St. Helena, South Africa, New Zealand, S. Australia). Lozano Rey 1947:597 (in part; New Zealand and South Africa in range). Smith 1949 (and 2d ed., 1953):129, fig. 224 (along most of South Africa; remarks). De Buen 1950:92 (in part; reference to Montevidéo reports). Fowler 1956:141-142 (characters; in part; South Africa; Indo-Pacific). López 1957:145-151, fig. 1-8 (synonymy and records for South American Atlantic; mouth of Río de la Plata at 36°52′ S, 54°02′ W; development of beak; mucus canal system of head; digestive canal). Briggs 1958:264 (Atlantic, Indian, and western Pacific Oceans; in western Atlantic to Argentina). Wheeler and Mistakidis 1960:334 (in part; Tristan da Cunha, record only). Clemens and Nowell 1963:253-255 (17°30′ S, 71°30′ W; 20°25′ S, 70°43′ W). Hotta 1964:4-7, fig. g. 2-5, table 1 (in part; distribution mapped, southern oceans). Parin and Gorbunova 1964:224 (translation, 1966:237) (Indian Ocean; mentions *S. saurus* having pelagic eggs in open ocean, reference to Haeckel 1855 and Sanzo 1940). Parin 1967a (translation 1971): many pages (in part; epipelagic fish; distribution in Pacific; development); 1967b:150 (117 in translation) (among most plentiful fishes in moderately warm waters of both hemispheres; larvae common at surface day and night). Penrith 1967:524, 544-545 (Tristan da Cunha, at 37°05′ S, 17°40′ W [error for 12°17′ W]; surface-living). Rass 1967:58-66, fig. 10 (in part; distribution in Pacific; general remarks). Parin 1968b (and translation 1970): many pages (in part; world distribution in epipelagic zone); 1968a:275-290, fig. 2-5 (in part; development and numbers of gill rakers; distribution, with records; synonymy); 1969a:719, fig. (in part; place in high-seas fauna; distribution mapped in North Atlantic and in Southern Hemisphere); 1969b:577, 579 (462, 464 in translation), fig. 2 (in part of area surveyed off west coast of South America; numerical abundance charted). Ueyanagi et al. 1969:6-7, fig. 12 (occurrence in all southern oceans). Tortonese 1970:366 (in part; temperate region of whole ocean). Ben-Tuvia 1971:10, 29, 35 (cosmopolitan [in part]). Ueyanagi and Doi 1971:17-21, fig. 15 (distribution in southeastern Pacific mapped; characters distinguishing juveniles of *Cololabis adocetus*, *C. saira*, and *S. saurus*). Parin and Andriashev 1972:963 (866 in translation) (along 26° W between 37° and 39° S, and along west profile off South America between 34° and 45° S; temperature from 14.3° to 20.4° C). Chigirinsky 1972:151-165, fig. 1-13 (size and composition in southeastern Pacific); 1973:198-215, fig. (in part; "winter" range 5°-7° S in southeastern Pacific; spawning intermittent throughout year; stock and catch estimated). Ueyanagi et al. 1972:15-19, fig. 1-2 (size of fish graphed; distribution in Atlantic Ocean mapped). Parin 1973:261-262 [in CLOFNAM] (in part; southern

[9]Fowler entered, under the species name, merely "Brasil (Ribeiro, 1915)," but Miranda-Ribeiro (1915), in his Fauna Brasiliense, Scombresocidae, p. 21, the 16th or 22d page of the book, gave as the basis for including the species in his treatise on Brazilian fishes the range statement: "... habita o Atlantico desde Cap. Cod. na America do Norte, costas da Europa e da Africa e foi constatado em aguas de Montevidéo pelo Dr. Carlos Berg." This circumstance was probably the basis for the listing of the Scomberesocidae in Brazil by Fowler (1942b:384).

form in synonymy; reference to Parin's (1968a) use of *S. s. scombroides*). Suda 1973:2134-2135, fig. 7-9 (in part; distribution of larvae and preadults; potential fishery). Kawamura 1974: many pages (in food of southern sei whale; seems to swarm at surface, probably at patches of crustacea on which it may feed). Kusaka 1974:26, 111, fig. 163 (urohyal of 318 mm specimen from off Cape Town similar to that of *C. saira*). Dudnik 1975a:203-210 (182-188 in translation), fig. 1-2 (limits of distribution of larvae, fingerlings, and juveniles in winter in South Atlantic from South America to Africa); 1975b:738-743 (503-506 in translation, in which names were misspelled *Scombresox* and Scombresocidae), fig. (*S. saurus* compared with *Scomberesox* sp. Parin [= *Nanichthys simulans*]; distribution in Atlantic Ocean). Robertson 1975:7, 18, fig. 4a (planktonic egg; offshore waters around New Zealand). Smith 1975:22 (southern Africa; Afrikaans and English vernaculars). Wheeler 1975:324 (circumpolar in Southern Hemisphere; off South America, South Africa, South Australia, and across Pacific to American continent). Paxton *in* Allen et al. 1976:387 (references; circumglobal in Southern Hemisphere, including eastern Australia and New Zealand as *S. forsteri*; North Atlantic and Mediterranean).

Sairis scombroides.—Richardson 1842:26 (synonymy; valid characters adopted[10] verbatim from manuscript on "*Esox scombroides*, Solander, p. 40; *Esox saurus* G. Forster [MS], ii. t. 233; J. R. Forster, MS II 65, apud Bl. Schneider, p. 394 . . . lat 39½° S, 204¼° W, [sic] between New Zealand and New Holland . . . . The specimen figured by G. Forster was captured . . . in Dusky Bay [New Zealand]. The aborigines named it 'he-eeya.' ").

Scombresox scombroides.—Scott 1962:77, 1 fig. (brief description; western and southern Australia, Victoria, New South Wales, and Tasmania; vernaculars).

Scomberesox saurus scombroides.—Parin 1968a:284 (tentative name for Southern Hemisphere subspecies of *S. saurus*, based on fewer gill rakers). Chirichigno F. 1974:90, 318, 349, fig. 18-19 on p. 91 (characters in key; Punta Aguga, Perú, to Chile; Isla Juan Fernández and [in error] Isla de Pascua).[11]

Scombresox Rondeletti (misidentification on subspecies level).—Valenciennes 1846:475 (in part; Cape of Good Hope record only). Bleeker 1860:56 (Cape of Good Hope only).

Scomberesox rondeletti.—Gilchrist 1901:152 (South Africa).

Scombresox equirostrum (misidentification on subspecies level).—Valenciennes 1846:479-481 (description based on specimen from Chile reported by Guichenot in 1848). Guichinot 1848:318-319 (description; rarely found in Chile). Rendahl 1921:50-51 (Isla de Juan Fernández; also off Perú, New Zealand, southeast Australia, and [in error] Japan).

Scomberesox equirostrum.—Fowler 1940:757, fig. 27 (Valparaíso); 1944a:491 (Valparaíso and Isla de Juan Fernández, Chile); 1944b:30-31 (synonymy; republished in book form under same title, 1945:78-79). Mann 1950:25 (key; distribution, Arica to Valparaíso, Islas de Juan Fernández; found in markets of central Chile, May-July; vernaculars). Fowler 1951:282 (in key; Chile). Mann 1954a:47, 79, 169-171 (description; distribution; restricted to pelagic warm water, Arica and Islas de Juan Fernández and [in error] Isla de Pascua; vernaculars); 1954b:77 (listed off Chile in subtropical waters). De Buen 1955:154 (listed off Chile as food of *Germo alalunga*).

Scombresox aequirostrum.—Günther 1866:258 (references; Chile; Chilean fish described by Valenciennes may prove distinct). Reed 1897:18 (listed for Chile). Delfin 1900:4 (listed for Chile; generic name misprinted as *Scombresose*). Quijada 1912:95 (Valparaíso).

Scomberesox aequirostrum.—Delfin 1901:45 (synonymy; in part; Islas de Juan Fernández). Quijada 1913:84 (listed for Chile; edible; commercial importance).

Scomberesox storeri.—Storer 1853:268 and 1867:137-139 (status of LeSueur's "*S. equirostrum*" from Chile).

Scombresox forsteri.—Valenciennes 1846:481-482 (original description [indicated by "nob"]; received from Forster; New Zealand). Günther 1866:258 (synomy; diagnosis; validity doubted; New Zealand). Hector 1872:118 (rare in New Zealand waters; compared with "Half Beak").

[10]Not all "nomina nuda" as stated by Whitley (1968:35); applicable characters were given.

[11]The Isla de Pascua record of a 480 mm "Scomberesox" listed by Wilhelm and Hulot (1957:148) was referred to *Belone (Eurycaulus) platyura* by de Buen (1963a:16), who, we presume, examined the specimen (43C).

Macleay 1881:244 (description; Melbourne and Sydney). Günther 1889:34[12] (unable to separate young of *saurus* and *forsteri*). Hutton 1872:53 (description; 12-in specimen; New Zealand); 1889:283 (New Zealand). Sherrin 1886:305 (New Zealand). Hutton 1904:50 (New Zealand). Stead 1906:70 (Australia); 1908:39 (characters; immense shoals of half-grown fish inside Port Jackson Heads). Regan 1916:134 (northern New Zealand and Three Kings Islands). Phillipps 1921:120 (food value; highly esteemed edible fish at Bay of Islands; probably spawns in mid-May). Waite 1921:64 (South Australia; often netted with garfish); 1923:88, fig. 96 (length to 15 in; surface skipping and jumping).

Scomberesox forsteri.—Brevoort 1856:281 (New Zealand; seems closest to *S. saira*). Jordan et al. 1930:197 (questioned synonymy with *S. saurus*; New Zealand). Munro 1938:55, fig. 389 (diagnosis; habitat: New South Wales, Victoria, Tasmania, South and West Australia). Berg 1939:207, and 1941 (reprint):654 (closely repeated species; New Zealand and southern Australia). Whitley 1948:15 (off Albany and Perth, Western Australia). Andriashev 1961:345, 348—as "*Scomberesox forsteri*"; 397, 422, 424, 442—as "*Scomberesox*"; 421, 426, 442, 443, 445—as "*Scomberesox* sp" (taken at "Ob" stations in southern Pacific Ocean); 1962:285 (north of 46° S in "Zone of *Scomberesox*"). Whitley 1962:52, fig. (habits; characters; southeast Australia, New Zealand, and Tasmania to West Australia, and elsewhere). Moreland 1963:18, fig. (general remarks). Parin 1963:134, 139 (attracted to light at night). Heath and Moreland 1967:16, fig. 17 ("needlefish" and other vernaculars; general remarks; New Zealand). Parin 1967a:58 (42 in translation) (doubtful status as species). Berman and Ryzhenko 1968:10, 12, fig. (young and adults off Chile and Perú; potential fishery). Whitley 1968:35 (synonymy). Scott et al. 1974:88 (description; distribution; West and South Australia, Victoria, New South Wales, and Tasmania; uncommon off South Australia).

Scomberesox saurus forsterii.—Chirichigno F. 1969:40, fig. 85 (vernaculars; Perú, Chile, Islas de Juan Fernández; detailed description).

Scomberesox stolatus.—de Buen 1959:262-264 (original description; synonymic references to *Scomberesox* and *Scomberesox equirostrum* and *aequirostrum*; types from 35°20′ S, 75°23′ W; vernaculars). Chirichigno F. 1962:2, 8-9, fig. 6 (Callao and Isla Chincha, Perú; from Arica to central zone of Chile; Islas de Juan Fernández, and [in error] Isla de Pascua; not previously known from Perú). Koepcke 1962:196-197 (references; high seas; west coast of South America from central Chile to Callao, Perú; Islas de Juan Fernández, and [in error] Isla de Pascua [see footnote 11]). De Buen 1963b:81, 83, 85 (key; brief description; Antofagasta). Medina 1965:260-261 (habitat; central Chile from Callao, Perú, and Juan Fernández Islands, and [in error] Isla de Pascua).

Cololabis saira (misidentification).—Chirichigno F. 1962:9, fig. 7 (description of young; Paita, Perú). Koepcke 1962:197 (in part; reference to Chirichigno's Paita record only). Fourmanoir 1971:492 (87 specimens, 8-30 mm, from 180 mi west of Port Macquarie, New South Wales, Australia).

Scomberesocidae.—Lönnberg 1907:15 (Straits of Magellan, "Smyth Channel, Eden Harbour"). Fowler 1942b:384 (Brazil, Patagonia, West Africa).

Scomberesox.—Böhlke 1951:85-86 (Chile; *Cololabis adocetus* compared).

Needlefish.—McKenzie 1964:14, 1 fig. (in part; vernaculars; color; size; habits; New Zealand).

Discussion of Synonymy.—The synonymy of *Scomberesox* has some complications but in general is relatively clear taxonomically and nomenclaturally. The name was spelled as *Scomberesox* twice by Lacépède (1803), hence can hardly be treated as a misprint, though in naming the species *Scomberesox Camperii* he gave the French vernacular as *Scombresoce camperien*. Many authors, beginning apparently with Rafinesque (1810), adopted the classically more correct but unacceptable (unauthorized) emended spelling *Scombresox* for the genus, and this spelling is still occasionally followed in Europe (viz. Zoological Record (Pisces), 1956-59). The type-species of *Scomberesox*, by monotypy, is *S. camperii* Lacépède, a synonym of *S. saurus saurus* (Walbaum).

[12]Günther referred the pelagic fry and young sauries ("up to 1⅗ inches in length"), taken in the Pacific Ocean, to *S. forsteri*, while acknowledging that he could not distinguish them from *S. saurus*. But he stated that these specimens were taken in July 1875, during which month the ship was running east from Japan near 35° N, thence due south to Hawaii (Mosely 1879:495 and track chart; also p. 750 and Sheet 36 of Part 1 of Vol. 1 of Challenger Report). Although the specimens are apparently not extant in the British Museum (see footnote 5), it seems safe to conclude that the record was based on *Cololabis saira*.

The earliest synonym, *Sayris*, was proposed by Rafinesque (1810), with the statement: "Cosrisponde al genere *Scombresox* di Lacepede, il di cui nome essendo formato dall'unione di due altri nomi generici e talmente contra la leggi della nomenclatura zoologica, ..." Since *Sayris* was obviously proposed as a replacement name for *Scomberesox*, it takes, according to Article 67 (i) of the International Code, the same type-species, namely *Scomberesox camperii* Lacépède. The type-species has been designated (Jordan and Evermann 1896) as *Sayris* "*recurvirostra* = *camperi*," obviously on the basis of the original indication of *Sayris recurvirostra* as a replacement name for *S. camperii*. This type of designation was repeated by Jordan (1917). Jordan et al. (1930) gave the type as "*S. recurvirostra* Rafinesque = *Esox saurus* Walbaum," but *Camperii* is not an objective synonym of *saurus*.

Gramminocotus Costa (1862) is clearly a subjective synonym of *Scomberesox*. The type-species, by monotypy, is *G. bicolor*, an obvious synonym of *Scomberesox saurus saurus*. The statement by Jordan et al. (1930) that *Grammiconotus* is "said to lack the air bladder" seems to have no basis other than the erroneously indicated lack of the gas bladder as a character of *Scomberesox* in the Mediterranean, from which the 40 mm type of *G. bicolor* came. Various authors have reported on the presence or absence of a gas bladder in *S. saurus* from the Mediterranean. Valenciennes (1846) based *S. Rondelettii* on the belief that it had no gas bladder; Günther (1866:258) and Moreau (1881) accepted this action. Lütken (1880) and subsequent authors accepted the presence of the bladder, but Supino (1935) failed to find it. Scordia (1936, 1938) found it in specimens from Messina and Naples. Further supporting its presence, Enrico Tortonese[13] stated: "Personally, I believe it is present, as I have found it in all the dissected specimens from Nice and Genoa. Its walls are thin and easily broken; this may perhaps explain why it was sometimes overlooked." One of us (Wisner) has found the gas bladder in a 197 mm SL subadult from the Straits of Messina, as has N. B. Marshall[14].

There was also no basis for the indication (Jordan 1921) that the genus *Grammiconotus* lacks a beak (it had not yet elongated in Costa's type, "Long. corp. millim. 40"). The generic recognition by Jordan and by Golvan (1962, 1965) was an anachronism.

JUSTIFICATION OF SUBSPECIFIC SEPARATION

Parin (1968a) reported differences in the numbers of gill rakers of *Scomberesox saurus* between 7 specimens from the North Atlantic and Mediterranean (average 40.75) and 64 specimens from the Southern Hemisphere (average 44.67). On this rather limited basis he concluded that the two populations may be separable, at least at the subspecific level, and, if so, the southern subspecies should be named "*S. saurus scombroides* (Richardson)." Parin also stated: "There are no significant morphological differences between populations inhabiting southern regions of the Atlantic, Indian and Pacific oceans." We concur in this latter statement and include populations from the Northern Hemisphere (not included by Parin, perhaps due to limited material, seven specimens). Furthermore, we agree with Parin that the populations of the two hemispheres may be separable as subspecies and that the name *Scomberesox saurus scombroides* (Richardson 1842) is applicable to the Southern Hemisphere form.

While we are aware of the highly subjective criteria for subspecific separations, and despite the extensive overlap in counts of gill rakers between populations of the two hemispheres (Table 7), we favor the distinction of the two populations as subspecies. We base this action both on probably highly significant statistical differences (untested) in numbers of rakers and on the presently known distribution of the genus (see below). We cannot conceive of any recent intermingling across the equatorial region of the Atlantic Ocean, at least since the glacial period; the species does not occur in the North Pacific, and, presumably, the northern Indian Ocean is too warm for it.

The statistical reasoning on which we base subspecific distinction involves both a method of graphical analysis of variation (Hubbs and Perlmutter 1942, revised by Hubbs and Hubbs 1953) (Figure 6) and a value, "coefficient of difference (C.D.)," from Mayr et al. (1953); this latter value is derived by dividing the difference between means by the sum of their standard deviations.

[13] Enrico Tortonese, Director, Museo Civico di Storia Naturelle, 16121 Genova, Via Brigata Liguria N. 9, Italy, pers. commun. 8 July 1968.

[14] N. B. Marshall, Curator of Fishes, British Museum (Natural History), Cromwell Road, London SW7, England, pers. commun. 21 June 1968.

TABLE 7.—Numbers of gill rakers, by areas, for the two *Scomberesox saurus* subspecies.

	Scomberesox saurus saurus				*Scomberesox saurus scombroides*					
							South Pacific[2]			
Gill rakers	Northwest Atlantic[1]	Northeast Atlantic	Mediterranean[1]	Total	Southwestern Central Atlantic	Atlantic near South Africa	New data	Parin (1968a)	Indian Ocean[1]	Total
34	—	1	—	1	—	—	—	—	—	—
35	1	2	2	5	—	—	—	—	—	—
36	4	4	3	11	—	—	—	—	—	—
37	6	1	2	9	—	—	—	—	—	—
38	8	5	4	17	—	—	—	—	—	—
39	13	—	5	18	—	—	5	1	—	6
40	13	4	3	20	—	—	10	2	—	12
41	13	2	3	18	—	1	23	4	—	28
42	3	1	2	6	1	6	21	5	3	36
43	5	—	—	5	1	4	34	7	1	47
44	2	1	—	3	2	10	19	2	8	41
45	1	—	—	1	6	8	17	4	6	43
46	—	—	—	—	11	4	10	3	7	35
47	—	—	—	—	4	5	5	2	3	19
48	—	—	—	—	2	3	3	1	2	11
49	—	—	—	—	4	3	—	3	1	11
50	—	—	—	—	1	1	—	1	1	4
51	—	—	—	—	1	1	—	1	—	3
N	69	21	24	114	35	46	147	36	32	296
$\bar{x}$	39.70	38.24	38.58	39.19	46.29	45.13	43.01	44.17	45.28	44.11
SD	2.13	2.61	2.08	2.28	1.93	2.38	2.35	2.95	2.76	2.52

[1]Counts by Parin (1968a:280, fig. 3) for specimens 75 mm and longer are included in the above counts for Northwest Atlantic (5 specimens) and Mediterranean (5 specimens).
[2]Data from Peru, Chile, Central Pacific, and Australia-New Zealand are combined since counts from each area are very similar, the means ranging from 42.87 to 43.08 gill rakers.

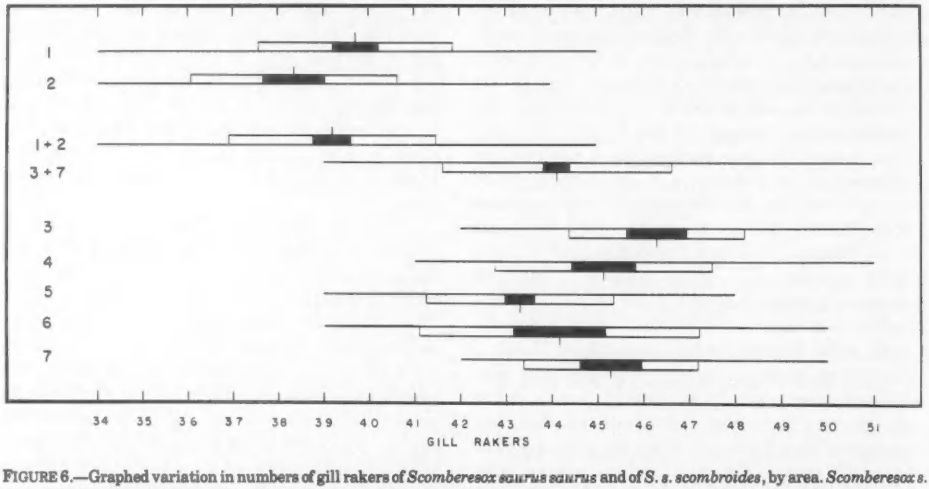

FIGURE 6.—Graphed variation in numbers of gill rakers of *Scomberesox saurus saurus* and of *S. s. scombroides*, by area. *Scomberesox s. saurus*: 1—Northwest Atlantic, $N = 69$; 2—Northeast Atlantic and Mediterranean, $N = 45$; 1 + 2—total for Northern Hemisphere, $N = 114$. *Scomberesox s. scombroides*: 3 + 7—total for Southern Hemisphere, $N = 296$; 3—Southwest-central South Atlantic, $N = 35$; 4—Atlantic near South Africa, $N = 46$; 5—South Pacific (new data), $N = 147$; 6—South Pacific (Parin 1968a), $N = 36$; 7—Indian Ocean, $N = 32$ (26 from Parin (1968a), 6 new data). In each sample the baseline shows the total range in variation, and the short vertical line the mean of the sample; open (white) bars delineate 1 SD on each side of the mean, and the solid (black) bars 2 SE of the mean on each side of the mean.

The difference between means for gill rakers (39.19 vs. 44.11) of the total populations of *S. s. saurus* and *S. s. scombroides* (Table 7; Figure 6, lines 1 + 2 and 3 + 7) appears to be highly significant, the probable odds (untested) being billions to one against the two areas comprising a single, homogeneous population. Despite a large overlap in numbers of rakers, the calculated C.D.

value is 1.025, a value approaching subspecific distinctness (as interpreted by Mayr et al.), in that it indicates a joint nonoverlap of about 85%. Of even greater significance, perhaps, is the difference in means (7.93 rakers) between populations from the southwestern-central Atlantic and the combined northeastern Atlantic-Mediterranean areas (46.29 vs. 38.36 rakers); the graphed data (Figure 6, lines 1 and 3) indicate again probable odds (untested) of billions to one that the two populations are not homogeneous; in addition, the C.D. value of 1.88 indicates about 99% joint nonoverlap in numbers of rakers—virtually that of separation at the species level.

As sampled (Table 7, Figure 6), the total population of *S. s. saurus* appears to be relatively homogeneous, but that of *S. s. scombroides* may be less so. Heterogeneity of populations in the Southern Hemisphere is indicated by a difference of 3.28 rakers between the areas of southwestern-central South Atlantic and the entire South Pacific (new data) (46.29 vs. 43.01); this may indicate that little or no intermingling occurs around the tip of South America. Conversely, the close agreement in means for rakers between specimens from the South Atlantic near South Africa and from the Indian Ocean (45.13 vs. 45.28) may indicate that considerable, if not complete, intermingling occurs around South Africa. The entire South Pacific area (as sampled) appears to contain a homogeneous population; a difference of only 0.21 rakers was found between samples of about 50 specimens each from the Peru-Chile, central, and Australia-New Zealand areas.

DESCRIPTION OF GENERA AND COMPARISONS

Inasmuch as we treat each of the four obviously distinct saury species as constituting a monotypic genus, the comparisons of these genera, as previously discussed, and epitomized in Table 1, provides a comparison of *Nanichthys simulans* with each of the three other scomberesocid species. It certainly ranks as one of the two dwarfed species. The largest specimens of this species examined by us were taken in Funchal Harbor, Madeira (126.2 mm SL, Museo do Funchal No. 2866, shown in Figure 1, and 121.2 mm SL, BMNH 1953 · 3 · 13 · 7). No other specimens >101 mm SL (USNM 204257) have come to our attention and none other among hundreds examined by us have exceeded 90 mm. Parin (1968a) recorded 90 mm SL as the largest of his material. Dudnik (1975b) reported that the longest of about 200 specimens of "*Scomberesox* sp" was 112 mm. The occurrence of the two "giants" in Funchal Harbor leaves us to wonder if the inshore habitat may have led to increased or sustained growth. G. E. Maul[15] has told us that the genus is rare near Funchal.

Nanichthys simulans, unlike *Elassichthys adocetus*, has retained the lateral line; it extends to about midway between the origins of the pelvic and anal fins, but not, as in *Scomberesox* and *Cololabis*, to opposite some one of the anal finlets. The upper and lower jaws, instead of remaining short and pointed as they do in *Cololabis*, or short and rounded (in the upper) as in *Elassichthys* (Figures 5, 6), become definitely elongated as beaks, but remain shorter than in *Scomberesox*; the upper is about half as long and produced as the lower, and much less slender and fragile than they are in *Scomberesox*.

Counts for *N. simulans* are given in Table 2 (gill rakers), Table 3 (fin rays), and Tables 4 and 5 (vertebrae), and are contrasted with similar data for *E. adocetus* and for the larger forms, *C. saira* and *Scomberesox*; numbers of gill rakers are given for both subspecies of *Scomberesox* in Table 7.

The pectoral rays of *N. simulans*, numbering 10 or 11, average more than in *Elassichthys* (8-11, usually 9 or 10), but fewer than in *Cololabis* and *Scomberesox* (12-15 in each). The procurrent caudal rays number 4, rarely 3 or 5, vs. 2 or 3 in *Elassichthys* or 5-7 in *Cololabis* and *Scomberesox*. The vertebral counts are 58-62, mean 60.68, contrasting with 54-59, mean 56.37, in *Elassichthys*, 62-69 in 3,160 specimens of *Cololabis*, with means of 66.05 for 248 counts for the northwestern Pacific and of 65.03 for 2,812 counts for the northeastern Pacific, and 66-70, mean 66.13, for 338 counts for *Scomberesox* (both subspecies).

Scale counts (lateral midline rows) number 77-91 vs. 70-88 in the other dwarf species, *E. adocetus*, as mutually contrasting with counts of 128-148 in *Cololabis* and of 107-128 in *Scomberesox*. Counts of gill rakers in *Nanichthys* (19-26, mean 22.80) average higher than for *Elassichthys* (15-21, mean 17.64), but much lower than in either *Cololabis* (32-43, mean 37.53) or *S. s. saurus* (34-45, mean 39.19) and 39-51 (mean 44.11) for *S. s. scombroides* (Table 7). The ovary, as in *Elassichthys*, is single instead of paired (as

[15] G. E. Maul, Curator of Fishes, Museu Municipal do Funchal, Madeira, pers. commun. 5 May 1978.

noted below in the general description of the ovary in the two dwarf species).

In life *Nanichthys* is silvery ventrally and laterally, becoming greenish with brown specks dorsally; this is also the basic coloration of the other three genera. In preserved specimens the anal fin is essentially colorless, but the dorsal, pectoral, and caudal fins bear microscopic spots of dark pigment along the edges of the outer rays. The caudal fin, in addition, is pigmented in the crotches of the first branching of the rays and sometimes in the second branching of both dwarf species (the resulting streaking shows in Figures 5, 8, 9). In preserved specimens of this (and of other) scomberesocid species, a dusky underlying streak parallels the dorsal margin of the body (evident in Figure 5). *Elassichthys adocetus* has basically the same coloration.

JUSTIFICATION OF GENERIC SEPARATION

In recognizing a separate genus for each of the four species of Scomberesocidae we are cognizant of the circumstance that we are in a period when lumping is prevalent. We hold, however, that the grounds for the recognition of the four genera are compelling, and consistent with other generic recognitions on similar grounds. The distinctive features stand out sharply in the generic comparisons (Table 1).

The complete lack vs. strong development of the gas gladder and the single vs. paired ovaries, supplemented by a series of minor characters, primarily the striking differences in body musculature (Figure 7), and bolstered by the vast difference in body size, seem to provide fully adequate grounds for distinguishing both *Elassichthys* and *Nanichthys* from either *Cololabis* or *Scomberesox*.

The sagittal sections of the four genera of scomberesocid fishes (Figure 7A-D), taken from close behind the bases of the pelvic fins, portray these striking differences. The 59 mm SL adult of *Elassichthys* and 60 mm SL adult of *Nanichthys* clearly show the lack of the gas bladder; also, there is no evidence of even a weak septum that might indicate a paired condition of the ovaries. Even in the young of *Cololabis* (59.4 mm SL) and of *Scomberesox* (59.7 mm SL) the roughly triangular gas bladder is plainly evident just above the liver and gut; these young specimens are too immature to have recognizable gonads.

Also evident and notable is a difference in the arrangement of the myotomes; those of the young *Cololabis* and *Scomberesox* (and of adults) are separated by distinct septa. However, in the adults of the dwarf forms the myotomes are much more massive and the dividing septa are greatly reduced in number in *Nanichthys* (virtually nonexistent in *Elassichthys*). Perhaps this reduction is a reflection of the weak-swimming, surface-pelagic habits of these small fishes.

The development of filaments of a peculiar well-formed type on the egg of *Cololabis* strengthens the basis for the separation of that genus from *Scomberesox*, with unfilamented eggs. The large literature on *Cololabis* and its great commercial importance are additional incentives for retaining the familiar and well-established nomenclature; *Scomberesox* now approximates qualification in both categories.

The generic separation of the two dwarf forms also seems to be well justified. The feature of the well-developed beak in *Nanichthys* vs. its lack in *Elassichthys* (Figure 2) calls for generic separation, as it does for retaining *Cololabis* distinct from *Scomberesox*. The apparent total lack of an external lateral line in *Elassichthys* and its considerable development in *Nanichthys* provides sustaining evidence. Furthermore, the high probability that *Nanichthys* and *Elassichthys* are of separate origin (Figure 3), owing their resemblances to convergent evolution, seems to us clinching reason for generic separation.

Description of Gonads

The one ovary and the two testes of *Nanichthys* are essentially like those of *Elassichthys* (Figures 8, 9). Instead of being pendant from the dorsolateral walls of the coelom, they form, as they develop, a coherent median mass, occupying, with maturity, a very large proportion of the coelom from the middorsal line to the ventrally displaced liver, intestine, and other visceral organs. In the specimen figured for this discussion, the length of the ovary composes 38% of the standard length of the fish; the greatest depth of the ovary 20% of its length; and its greatest width 60% of its greatest depth.

The development of a single functional ovary in "*Scomberesox* sp" [= *Nanichthys simulans*] has been noted by Dudnik (1975b), who, however, mentioned that "the second [ovary] is rudimentary and can barely be discerned" [a translation]. We, however, have found not even a rudimentary

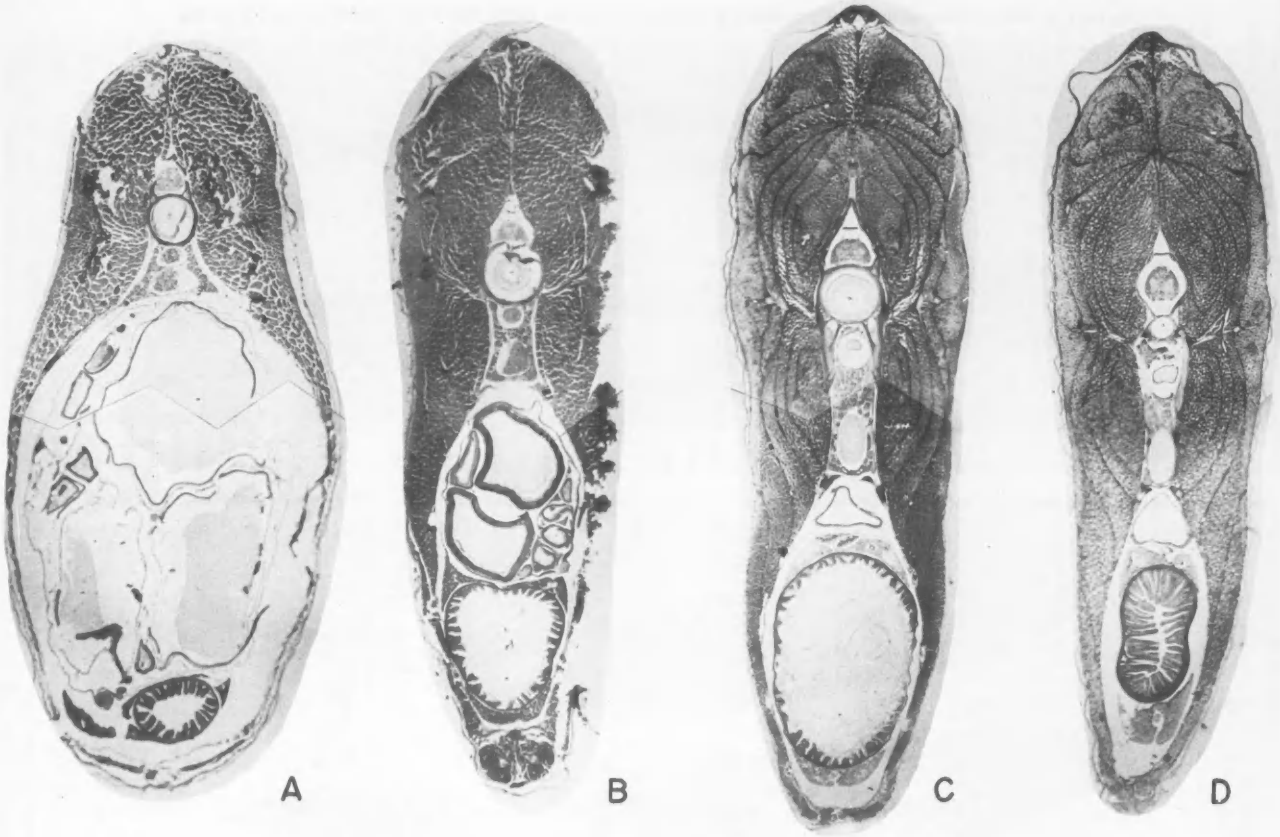

FIGURE 7.—Sagittal sections, taken from slightly behind origin of pelvic fin, of gravid females: (A) *Elassichthys adocetus*, 59.0 mm SL; (B) *Nanichthys simulans*, 60.0 mm SL; and of juveniles: (C) *Cololabis saira*, 59.4 mm SL; (D) *Scomberesox saurus*, 59.7 mm SL.

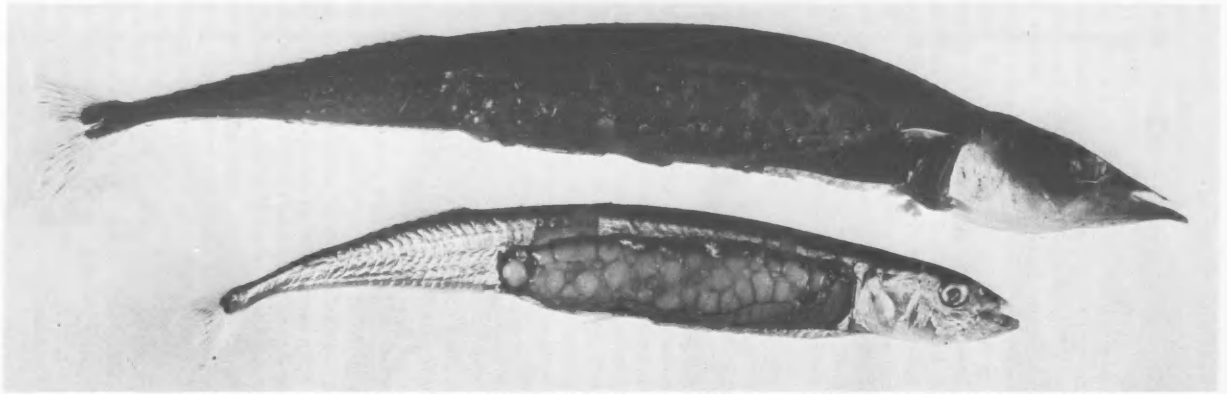

FIGURE 8.—Gravid single ovaries in situ: Upper—*Nanichthys simulans*, 85.5 mm SL; Lower—*Elassichthys adocetus*, 62.3 mm SL. Note the great range in sizes of ova.

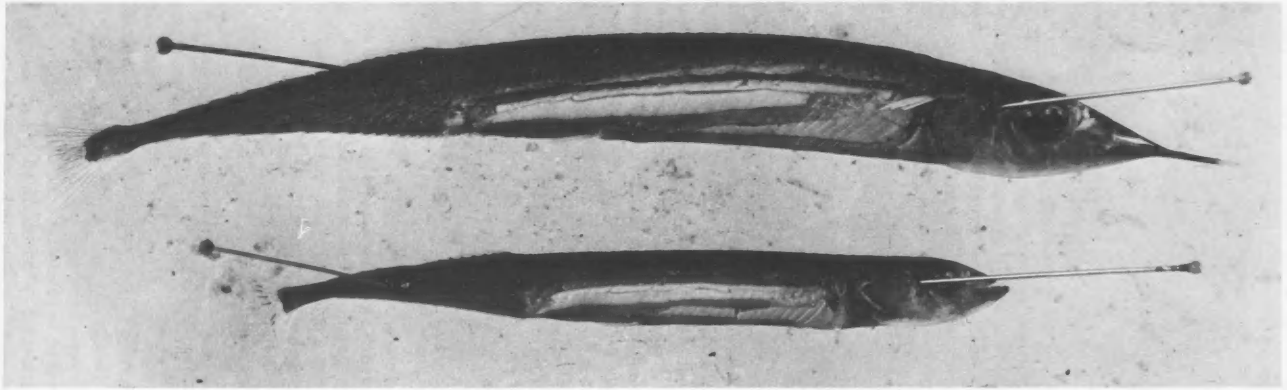

FIGURE 9.—Mature paired testes in situ: Upper—*Nanichthys simulans*, 90.0 mm SL; Lower—*Elassichthys adocetus*, 59.0 mm SL.

ovary in this species (nor in the other dwarf, *Elassichthys adocetus*).

In cross section the maturing and mature ovaries of both dwarfs are rather ovate in section. They very nearly fill the whole coelom between the much expanded body walls, particularly in *Elassichthys* (Figure 8). As they ripen, the ova fill the entire ovary so tightly that many of the ripe ova and even some of those in developmental stages are compressed into angular forms throughout the ovary. Forward, the ovary narrows dorsoventrally where the liver broadens to fill much of the coelom. Gentle probing readily discloses that the ovary lacks any structural connection with the coelom wall (except at the genital opening), although, with development, the ovary completely fills the body cavity above the visceral organs and lies closely appressed to the body wall, both dorsally and laterally. Dislodging the ova by probing discloses no trace of any internal septum.

The ova in the mature ovary of *Nanichthys* and *Elassichthys* appear on gross examination to represent at least four stages of development, but a major difference in size exists between the largest category (readily visible in Figure 8) and the next largest, as though an acceleration in growth precedes the extrusion of the brood. Since the ova of the largest category are usually markedly irregular in shape (presumably due to crowding), measurements are approximations. However, after discharge the ova are probably normally spherical rather than ovoid in shape, as the eggs of *Cololabis saira* have been described to be (Mito 1958; Mukacheva 1960). The largest egg size in the *Nanichthys* series studied ranged in diameter from 2.0 to 2.5 mm. The smaller and presumably younger size groups seemed to group around 0.80, 0.40, and 0.10 mm. Similar size groupings appeared to hold for *Elassichthys*.

The positioning of the largest eggs in the ovaries of the dwarfs seems to be quite random among the smaller ones (Figure 8). These large eggs were noted to be arranged generally mostly two abreast (three abreast once in *Elassichthys*). The random distribution of the large eggs within an ovary otherwise filled with smaller eggs invites speculation on how the anteriormost eggs of the largest size category move past the smaller ones to become extruded.

None of the eggs of the dwarfs, even of the largest and presumably soon-to-be-extruded category, show any sign of bearing filaments. Their surfaces, however, are sculptured with closely set, round, and extremely minute tubercles which are colorless (in preservative) and produce, under strong magnification, a finely pebbled effect.

It has not been determined whether the single ovary of the two dwarfed scomberesocids is the result of the fusion of bilateral primordia or is due to the failure to develop, or to the atrophy, of one ovary. The presence of but one gonad in synentognath fishes has been reported. Collette (1968) indicated that in the Belonidae *Strongylura marina* differs from a closely related species, *S. timucu*, in having only the right gonad developed. Collette (1974) reported that in the freshwater needlefish, *S. hubbsi*, 48 males had both testes developed but 2 apparently lacked the left one, and of 45 females, 2 had a tiny left ovary but all others lacked any trace of a left ovary.

In contrast with the ovary, the testis of both *Nanichthys* and *Elassichthys*, at apparent maturity, occupies only about one-third instead of about three-fourths of the height of the fleshy body (Figure 9). The testis agrees with the ovary, however, in occupying virtually the entire (limited) width of the coelom, forming from body wall to body wall a compact and compressed organ of seemingly homogeneous reproductive tissue. However, close inspection and some probing with a fine dissecting needle clearly discloses that the dorsally rounded mass comprises both testes. As seen from the right side, on removing the body wall (Figure 9), a fine, somewhat wavy longitudinal line, nearer top than bottom, indicates that the essentially homogeneous structure comprises the paired testes, and gentle probing confirms the indication. The left testis is definitely the larger, but both are well developed and are obviously functional. The two are essentially coterminal along the ventral edge, but the left testis definitely and sharply overtops the right. Ventrally the two organs form, at about the same level, symmetrical ridges on a rather broad base. At front, the paired testes are clearly distinct as lobes, of which the right one ends distinctly as a point, at that side of the left one. Anterior to the end of the right organ, the left one broadens on the ventral surface and forms a pair of bilaterally paired ridges, the left one of which seems to structurally replace the lost end of the right testis.

Mucus Pores and Canals of the Head

Numbers and arrangement of mucus pores and canals of the head vary notably among the scomberesocids (Figure 10, items 1-6). Adults of the two

larger forms, *Scomberesox* and *Cololabis* (Figure 10, items 1, 4), have a much greater number and complexity of pores and canals on the side and particularly on the top of the head, than do adults of the dwarfed forms, *Nanichthys* and *Elassichthys* (Figure 10, items 3, 6). Also juveniles of the larger forms (Figure 10, items 2, 5) show a greater pore-canal development than do the adult dwarfs, although they are of virtually identical size. This reduction of pores and canals in the dwarfs may be interpreted as an arrested state of development, perhaps neotenic or paedomorphic in character, as very small (20-24 mm SL) specimens of the larger forms bear a pore-canal structure similar to those of the adult dwarfs (Figure 10, items 3, 6); or, it may be that neither numbers nor complexity of pores is necessary at such small sizes and (perhaps) less active habits.

López (1957) provided the first figure of the pores and canals of the head of an adult (size not stated) *Scomberesox saurus* (= *S. s. scombroides*) from near Nechochea, Argentina. Our specimen, from the Perú-Chile area, bears a much greater profusion of pores and complexity of canals, particularly dorsally, than shown by López.

Collette (1966) illustrated interorbital canals and pores of four species of belonid fishes. These canals, rather simple and unbranched, which he reported to be representative of the Belonidae, are basically like those of *Elassichthys* and *Nanichthys*, although those of the latter show slight branching (Figure 10, item 3). Collette (his figure 7D) figured a complete joining of the left and right canals dorsally on *Belonion dibranchodon*, with both median and lateral pores present. He reported this condition to be unlike that of any other synentognath. Despite the profusion of pores and canals atop the heads of *Scomberesox* and *Cololabis* (Figure 10, items 1, 4), no joining of the left and right canals is apparent, although some canals very closely approach the median line.

Lateral Line Scales

The lateral line scales of *Scomberesox* and *Cololabis* are basically similar, but those of the dwarfed *Nanichthys* differ notably, both in shape and in numbers and development of circuli (Figure 11A-C). We have found no trace of lateral line scales in *Elassichthys*. All scales were removed from within 1 cm anterior to the pelvic fin. The basic similarity in the scales of the three genera involves the secondary tube on each scale that leads posteroventrally from the main tube and opens to the external surface of the scale. The primary (main) tube of each scale, in contrast, overlies the lateral line canal which extends along the body.

The lateral line scale of the adult *Scomberesox* (270 mm BL (body length); Figure 11A) lacks circuli, but they are present, though very weakly developed, on fish about 200 mm BL. Development of circuli appears to decrease as the fish grows; the circuli on scales on a 100 mm fish are notably better defined than on the 200 mm specimen. These early developed circuli occur in areas rather similar to those that are better developed in *Cololabis*. A principal feature distinguishing the *Scomberesox* scale from that of *Cololabis* is a well-developed baselike structure on the ventral aspect of the scale (Figure 11C). As the *Scomberesox* scale is much more tenacious than that of *Cololabis*, perhaps this structure serves as an anchor to the body. Another difference between the scales of *Scomberesox* and *Cololabis* is a narrow median band of tissue at about the center of the scale (and main tube) that does not absorb the weak solution of alizarin red S stain. When removing it, the highly tenacious scale usually breaks at this band. The *Scomberesox* scale figured is about 0.9 mm thick at the main tube.

The lateral line scale of the adult of *Cololabis* (262 mm BL; Figure 11B), in addition to differing in form from that of *Scomberesox*, differs in having at least weakly formed circuli on the anterodorsal and anteroventral aspects (these circuli do not show clearly, probably due to a slight canting of the scale during mounting and to the extremely short depth of focal field inherent in photomicroscopy). The scale has a thickness at the main tube of about 0.4 mm. The circuli are better developed on smaller fish and extend farther posteriad along both the ventral and dorsal aspects of the scale in about the same areas as in the adult scale. Some, but not all, lateral line scales of adults of *Cololabis* bear the nonstaining band of tissue found in *Scomberesox*, but it is much less strongly developed.

The lateral line scale of *Nanichthys* (106 mm BL; Figure 11C, from the 121.2 mm Funchal "giant") differs notably from that of its two larger relatives. The shape is quite different and the circuli are much more numerous and more strongly developed and extend over most of the scale, being absent only on the central portion of the basal (exposed) area. The thickness of the scale at the

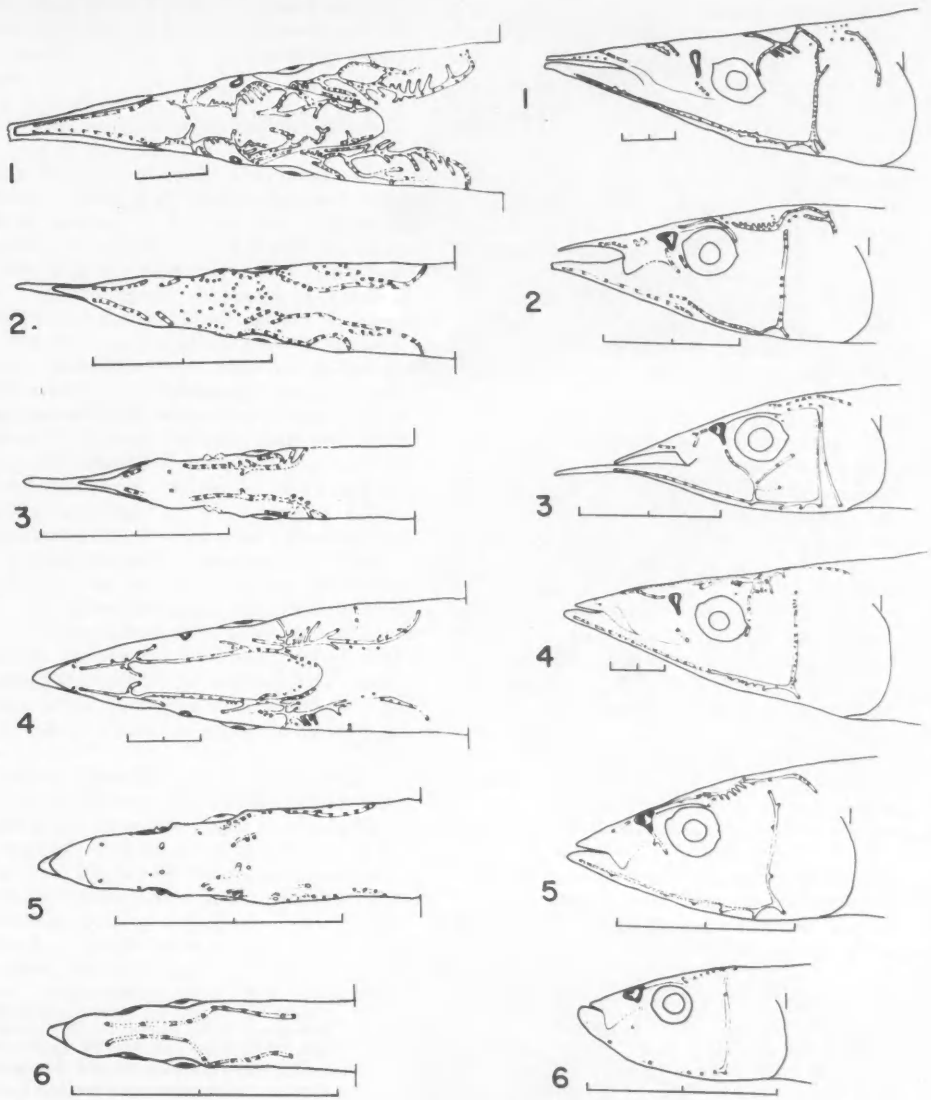

FIGURE 10.—Dorsal and lateral views of mucus pores and canals of heads of adults and young of scomberesocid fishes: (1) adult *Scomberesox saurus scombroides*, 240 mm BL; (2) young of *S. s. scombroides*, 70.8 mm BL; (3) adult of *Nanichthys simulans*, 70.0 mm BL; (4) adult of *Cololabis saira*, 243 mm BL; (5) young of *C. saira*, 54.0 mm BL; (6) adult of *Elassichthys adocetus*, 54.6 mm BL. Each scale line represents 1 cm.

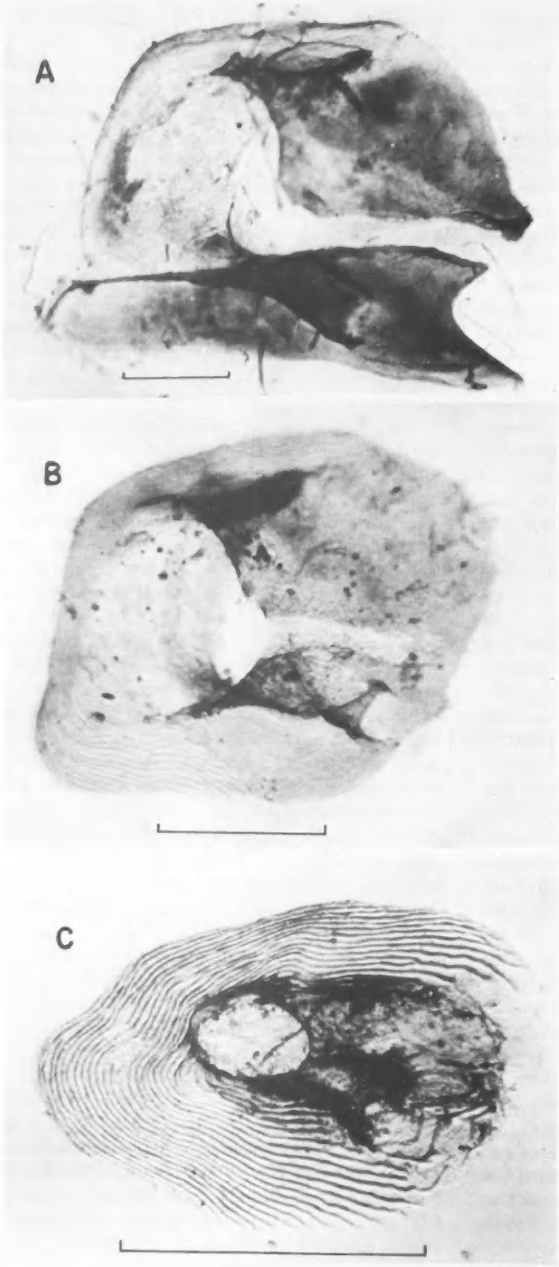

FIGURE 11.—Lateral line scales of adults: (A) *Scomberesox saurus scombroides*; (B) *Cololabis saira*; (C) *Nanichthys simulans*. The apical (covered) portion is to the left. All scale lines represent 1 mm. No lateral line scales have been found on *Elassichthys adocetus*.

main tube is about 0.1 mm. The tube is relatively more fragile than it is in the larger forms, and there is only a hint of the stain-resisting band of tissue.

Pharyngeal Bones and Teeth

The first pair of upper pharyngeal arches (bones) is absent in all the scomberesocid fishes. Also, the second pair of upper bones are so closely appressed as to appear as a single unit and are not notably larger than the third pair, which are not closely appressed; the lower pharyngeal bones are fused into one, as in the Synentognathi. Absence of the first upper pair of pharyngeals in synentognathous fishes has been reported by Collette (1966) who figured the pharyngeal bones and teeth of six species of the Belonidae: *Belonion dibranchodon*, *B. apodion*, *Potomarraphis guianensis*, *Strongylura notata*, *Pseudostylus angusticeps*, and *Xenentodon cancila*. Of these six, only *B. apodion* and *X. cancila* lack the first (lower) pair of upper pharyngeals; they also lack the second pair, retaining only the third (uppermost) pair. As figured by Collette, but not discussed, the pharyngeal teeth of these belonid species appear to have only a conical type of tooth, with no cuspate or lobate features. In apparent contrast, many of the pharyngeal teeth of the scomberesocid species treated below have more or less well-developed lateral lobes or cusps, or are distinctly tricuspid.

Cololabis saira, 281 mm SL, 225 mm BL, from the Gulf of Alaska (SIO 57-198). The greatest length of the lower pharyngeal arch is 12.8 mm, the greatest width 8.6 mm. The teeth are moderately strong and curved. The marginal ones are all slender and unicuspid but those within the margin in the wider part are definitely widened, slightly to greatly, medially, with usually on each side a marginal lobe grading from rudimentary to, rarely, a rather definite cusp. There is only a trace of alignment (the arrangement is more nearly quite indefinite). Along the interior, greatly narrowed half of the length, the teeth, reduced in size, are very roughly in three or four rows. The lateral teeth do not form a definite row and are not markedly enlarged. Toward the posterior margin the teeth are large and irregularly crowded. Most of the larger teeth bear a more or less well-developed median, lengthwise, rather rounded ridge.

Each bone of the second pair of upper pharyngeals is 11.8 mm long and 3.0 mm wide. Anteriorly and marginally the teeth are slender, moderately curved, and almost strictly unicuspid. Over the major portion of each bone, however, the teeth are, for the most part, definitely tricuspid, with the lateral cusps submedian and occasionally represented by weak to strong lobes. Between the left and right arches there is, posteriorly, a triangle of dermal ridges, medially a low ridge, and anteriorly a high ridge reaching to the surface with a strong fimbriation. As in the lower pharyngeal, the teeth are crowded and irregularly show just a trace of oblique seriation.

Each bone of the third pair measures about 2.3 × 6.7 mm. The teeth are nearly concealed in the strong fimbriation of the surface, and all are small, irregularly arranged, moderately curved, and unicuspid.

Elassichthys adocetus, 58.0 mm SL, 49 mm BL, from off Perú at 08°07′ S, 84°58′ W (SIO H 52-380). The lower pharyngeals are about 2.6 mm long and 1.1 mm wide. The teeth are relatively few, not more than about 10 across at the widest part of the arch. Most of the relatively large teeth in the median portion of the broad posterior region are broadened and to a varying degree tricuspid, with the central cusp much stronger than the lateral ones. The teeth along the posterior edge are rather broadly lanceolate rather than very slender as in *Cololabis*. Anteriorly, where the arch narrows, the teeth become weak. In the rows along the outer margins the teeth are relatively conical and moderately curved. The teeth across the posterior field are much larger than others and bear a median lengthwise ridge. Near the middle of the arch are only about four teeth in cross section.

Each bone of the second pair measures approximately 0.6 × 1.5 mm. The teeth are relatively robust and uniformly the sharp, definitely unicuspid tip is bent sharply. On the broad part of the bone there are only about five teeth in cross section. A membranous septum, very weakly patterned, extends the whole length between the two bones.

Each of the third pair of bones measures about 0.4 × 0.9 mm. The relatively few teeth are all unicuspid with the tips bent backward.

Scomberesox saurus scombroides, 290 mm SL, 205 mm BL, from off Chile, 34°30′ S, 79°30′ W (SIO 58-263). The lower pharyngeal has a midline length of 11.4 mm, a maximum width of toothed area (at posterior edge) of 7.3 mm, and a width

over teeth at midlength of 1.0 mm. The teeth are strongly heterodont and are rather definitely aligned, especially marginally, in rows. The teeth along the posterior margin number 41; those near the middle on each side are in nearly a single series alternating in proximity to the edge, whereas those toward either end tend to be arranged in oblique, separate rows of 2-4 teeth. All of these teeth are essentially erect, fairly stout, and pointed, with the tips not bent backward. The teeth along the two margins tend to form a rather even row; they are all sharply pointed, rather strongly bent backward, tend to flare outward, and are, in general, especially forward, larger and stronger than the teeth within; toward the anterior angles of the arch the marginal teeth tend to have a rather weak lobe on each side below the tip, and thus intergrade toward the median teeth. In the anterior half of the length of the arch the whole set of teeth grade from nearly triserial to uniserial, with only the very strong marginal teeth of each side occupying much of this space. After some intergradation, both anteriorly and laterally, the teeth occupying the major triangular part of the arch are dilated and bear on each side, well below the tip, a lobe or a cusp; they are strongly bent backward. Anteriorly the margins of the arch are rather strongly concave.

The length of each dental surface of the second pair is 8.9 mm; the maximum width of each, near the posterior end, is 2.7 mm. The teeth are arranged on each bone in about 16 rather regular rows extending from near the midline outward and backward in a weak curve. Teeth of reduced size, but otherwise similar, also curved, are found on a fimbriate pad immediately behind each bone. All of the teeth are bent backward. A number of teeth at the anterior end are simply conical, and especially strong. Virtually all of the other teeth, including those along the median and lateral edges, are tricuspid, with the median cusp very much stronger than the lateral pair, which arise well below the tip. The two bones are narrowly separated and a strongly fimbriate compressed membranous ridge intervenes, grading both forward and backward into several papillate rows.

The length of each bone of the third pair is 5.8 mm, the width of each 1.9 mm. The small teeth arise from a strongly papillate surface. They are directed mesiad and are strongest on the median margin, but definitely weakening laterally. They are all conical, without any trace of marginal enlargement.

Nanichthys simulans, 85.0 mm SL, 68.0 mm BL, from the central South Atlantic, 24°02.5′ S, 15°32.0′ W (SIO 63-546). The lower pharyngeal measures 1.9 × 3.3 mm. As in *Elassichthys*, but contrasting with the two large species, the arch is less attenuate forward and the posterior border is definitely convex instead of being slightly concave. There is no definitive alignment of the teeth, and a band about three or four teeth wide extends virtually to the front tip. The teeth rather regularly and strongly increase in size backward. About 20 teeth in one very irregular row, or in two rows, occur along the posterior margin; these are essentially erect, mostly very large, relatively, and show barely a trace of the lateral enlargements. Toward the front end the teeth are conical and less curved backward than the following teeth (excluding the posterior marginal ones). Most of the other teeth bear on each margin, well below the tip, either a lateral swelling or a definite cusp.

Each second pharyngeal measures 0.9 × 3.1 mm, with the greatest width well behind the middle. The teeth are scattered without definite alignment. Those in the narrow front end of the arch and those along the outer margin are conical or nearly so, with the tips bent backward, somewhat as in the other species. The remaining teeth, however, are vastly different, actually submolar. These rather lobular teeth seem to have been built on a much swollen and rounded version of the corresponding teeth in the other series, sometimes showing a trace of the lateral enlargements or cusps; but essentially they are irregularly rounded domes, but grading forward, outward, and backward into the more conventional, weakly tricuspid type.

Each third pharyngeal measures approximately 0.6 × 1.6 mm. The arch is widest behind the middle. The teeth are rather hidden in the papillae and all are simply conic, weakly curved backward. They are quite strong along the inner margin but grade into extremely minute ones on the outer margin.

DISTRIBUTION

The distributions of the scomberesocid fishes have been depicted by various Russian and Japanese authors. The Russian data are summarized by Parin (1968a, b, 1969a). Parin (1968a, b) received from us many of his data on "*Scomberesox* sp" (= *Nanichthys simulans*) and on *Cololabis adocetus* (= *Elassichthys adocetus*). Dudnik

(1975a) charted the distribution of *Scomberesox saurus* (= *S. s. scombroides*) in the South Atlantic Ocean, and (1975b) of *Scomberesox* sp. in the North and South Atlantic. Ueyanagi and coauthors have reported many captures of all the scomberesocid species, primarily juveniles and postlarvae, in the Pacific and Atlantic Oceans and the Mediterranean Sea.

In Figures 12-17 we attempt to show the known captures of all four species of scomberesocid fishes. In each figure the solid circles represent material examined by us. The large open circles in the North Atlantic and southwestern Pacific Oceans refer to literature records (specimens not seen by us); we have not used this symbol for literature records from the Pacific coasts of North and South

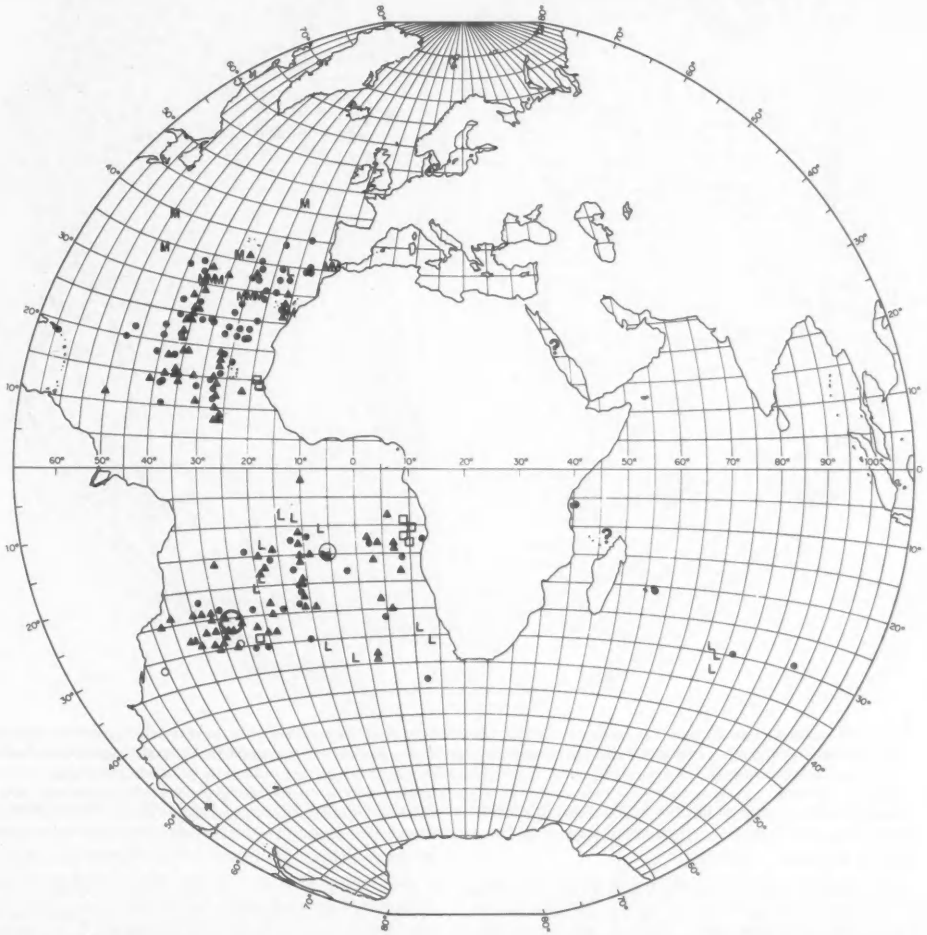

FIGURE 12.—Distribution of *Nanichthys simulans*. Solid circles represent material examined by us; solid triangles represent localities mapped by Ueyanagi et al. (1972); the large open circle in the southwestern Atlantic indicates 18 closely spaced collections (111 specimens), and the small open circles represent unpublished localities furnished by Parin; open squares refer to records mapped by Dudnik (1975b); letters L and M refer to records from Lampe (1914) and by Murray and Hjort (1912). The question mark near Madagascar represents Smith's 1955 record of *Scomberesox saurus* from Aldabra Island, which seems to represent this species. The query in the Red Sea refers to Borodin's 1930 record of a young "*Scomberesox saurus*."

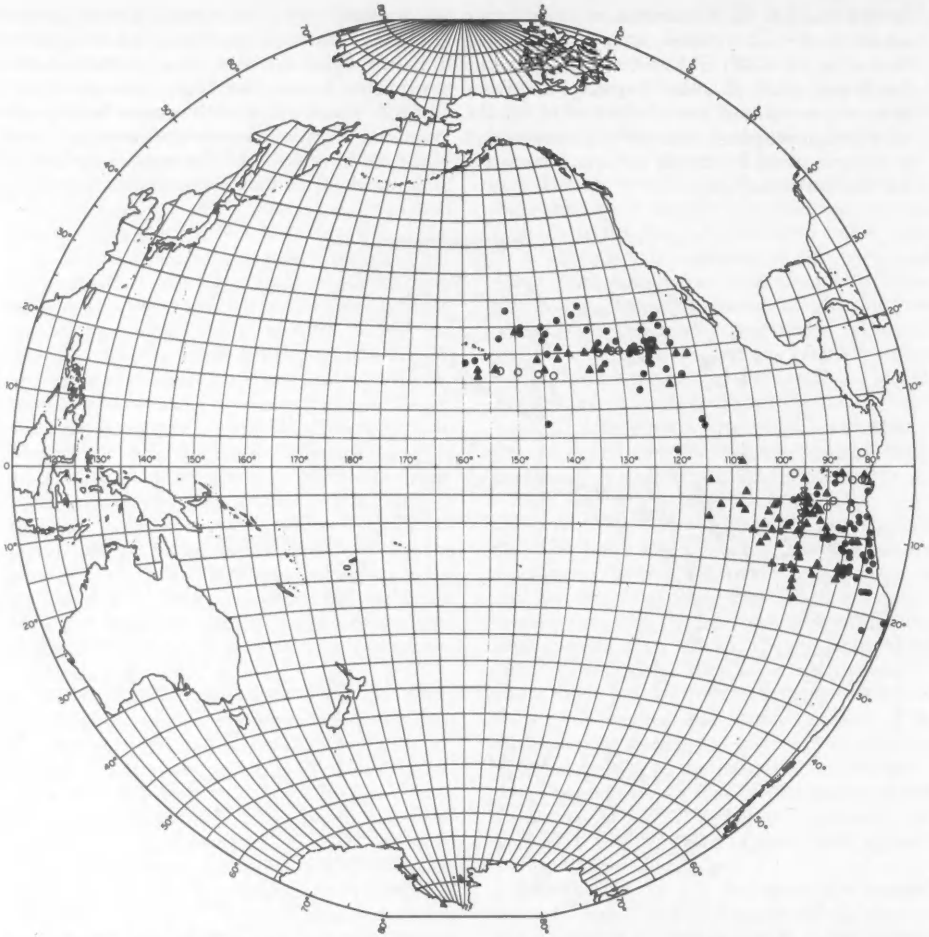

FIGURE 13.—Distribution of *Elassichthys adocetus*. Solid circles represent material examined by us; solid triangles, records mapped by Ueyanagi et al. (1972); open triangles, localities by Ahlstrom (1972); small open circles, unpublished records furnished by Parin.

America because either we have seen many of these specimens or have numerous captures from closely adjacent localities.

The sauries are essentially antitropical in distribution. This is particularly true for two larger forms, *Scomberesox* and *Cololabis*, which mostly inhabit cold to warm-temperate waters (Figures 14, 15). The dwarf genera *Nanichthys* and *Elassichthys* occupy much more tropical waters and occur much nearer the Equator than do their larger congenors. The one exception to this generalization is that of the northerly extension of juveniles and young of *S. s. scombroides* along the coast of Ecuador to about 02° S (Figure 15), where these young stages and the adults and young of *Elassichthys* have been taken together. This far northern extension of the young of *S. s. scombroides* is interpreted as due to transport by the northerly flowing Perú Current. Along the coast of Perú and northern Chile the ranges of *Elassichthys* and *S. s. scombroides* overlap to about 22° S (Figure 17).

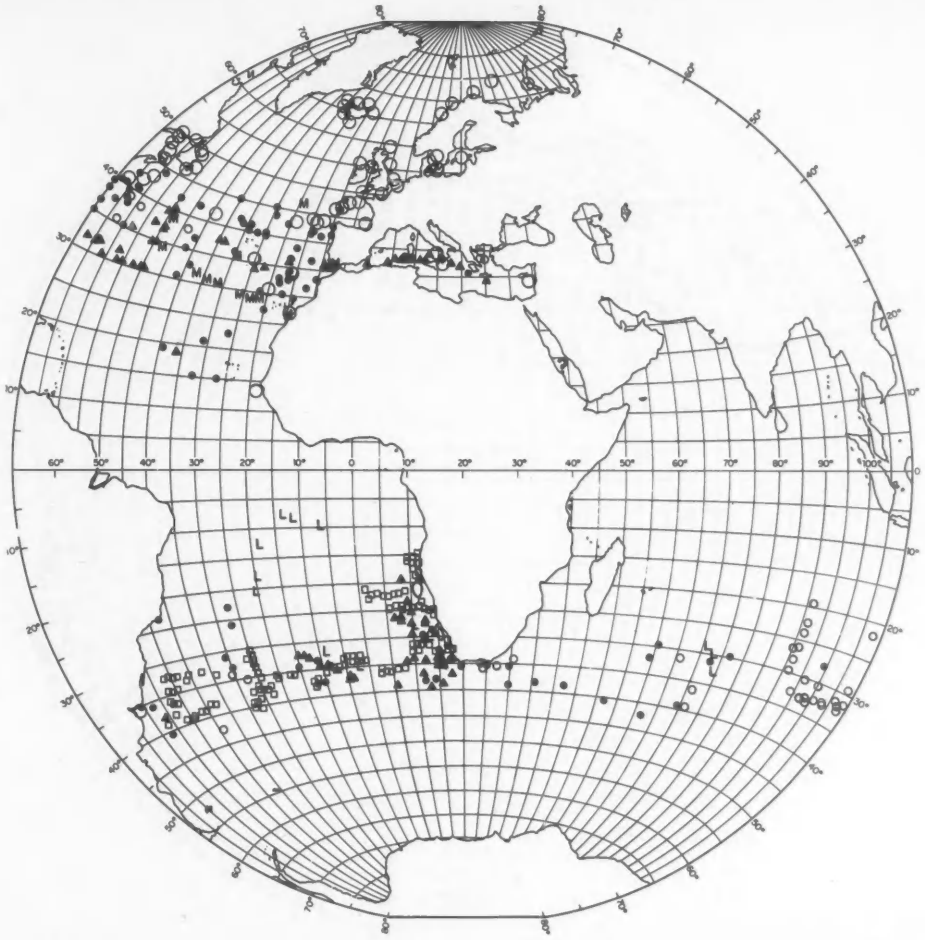

FIGURE 14.—Distribution of the northern and southern populations of *Scomberesox saurus* in the Eastern Hemisphere. Solid circles represent material examined by us; small open circles, records published by Parin (1968a); large open circles represent other published records (specimens not examined by us); solid triangles, records mapped by Ueyanagi et al. (1972); small open squares, localities mapped by Dudnik (1975a), additional and closely spaced records by Dudnik off southwestern Africa are indicated by two open ellipses. Letters L and M refer to records published by Lampe (1914) and Murray and Hjort (1912).

The far-southern locality off Chile for *S. s. scombroides*, at 47° S, 81° W (Figure 15), is based on seven juveniles (56-67 mm SL) in the Hamburg Museum (No. 10601) examined by us. This southern occurrence is not readily explained. It lies well within the portion of the West Wind Drift that forms the northerly flowing Perú Current; perhaps these specimens were waifs carried south into the edge of this current by the counterclockwise southeastern eddy of subtropical water that extends to between about 20° to 40°-45° S and 120°-80° W. The southern localities listed by Parin (1968a) to 48° S, about 110° W, are apparently attributable to a similar extension of subtropical water (Figure 15).

The questioned locality near the Straits of

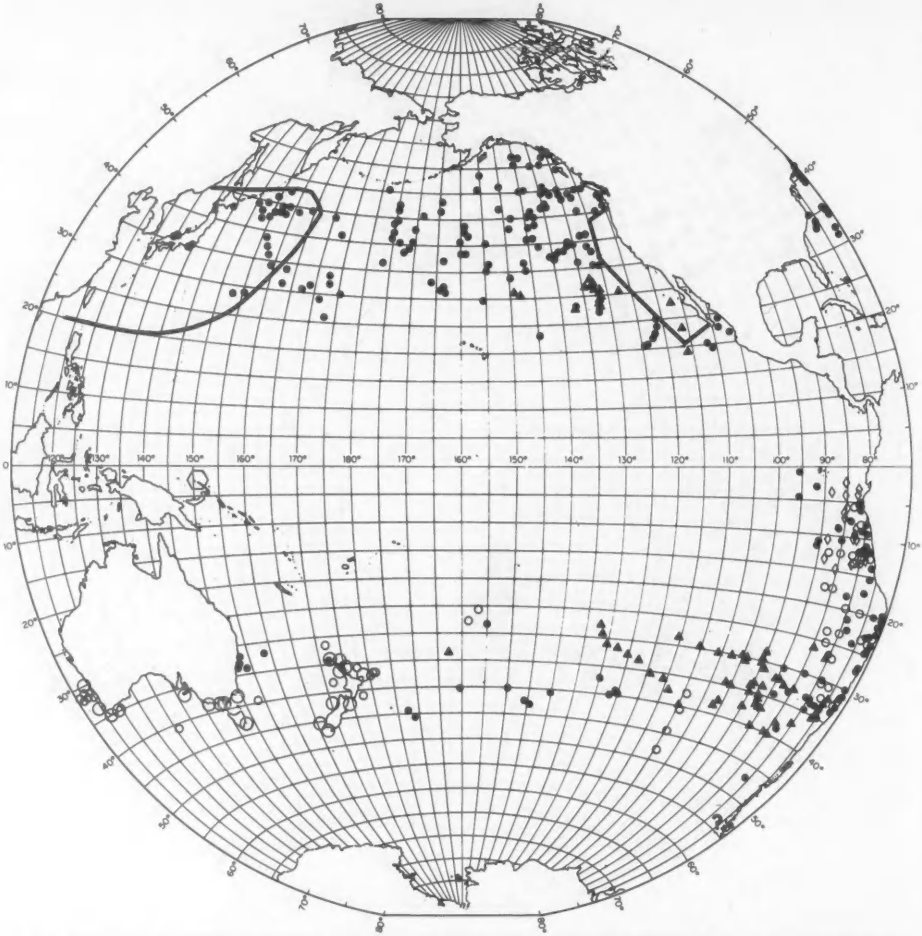

FIGURE 15.—Distribution of *Cololabis saira* and of *Scomberesox saurus* in the Western Hemisphere. Solid circles represent material of *C. saira* in the North Pacific, *S. saurus scombroides* in the South Pacific, and *S. s. saurus* in the extreme northeastern Atlantic Oceans examined by us. For the two areas bounded by heavy lines the records for *C. saira* would virtually blacken the areas and are omitted. Solid triangles refer to mapped records by Ueyanagi et al. (1972) for *C. saira* in the North Pacific and for *S. s. scombroides* in the south; small open circles represent both published and unpublished records of *S. s. scombroides* by Parin; large open circles are for other published records; open diamonds refer to records by Ahlstrom (1972). The question mark near Straits of Magellan refers to Lönnberg's (1907) record for a scomberesocid. The large open hexagon near New Guinea refers to the record of *C. saira* by Kailola (1974).

Magellan (Figure 15) refers to a statement by Lönnberg (1907) in a report on fishes from the Straits (Smyth Channel, Eden Harbor): "In der Sammlung befanden sich ausser den oben aufgeführten Spezies [*Macruronus magellanicus* n. sp.] noch Junge von mehreren Arten, die sich wegen der Jugend der Examplare nicht bestimmen liessen. Unter diesen fanden sich auch einige Repräsentanten für *Scomberesocidae*, so dass sich die Zugehörigkeit dieser Familie zu der magalhaensischen Fauna als sicher annehmen lässt." We question Lönnberg's identification of "Scomberesocidae" at a locality so far south, but we are at a loss to know with what other species his

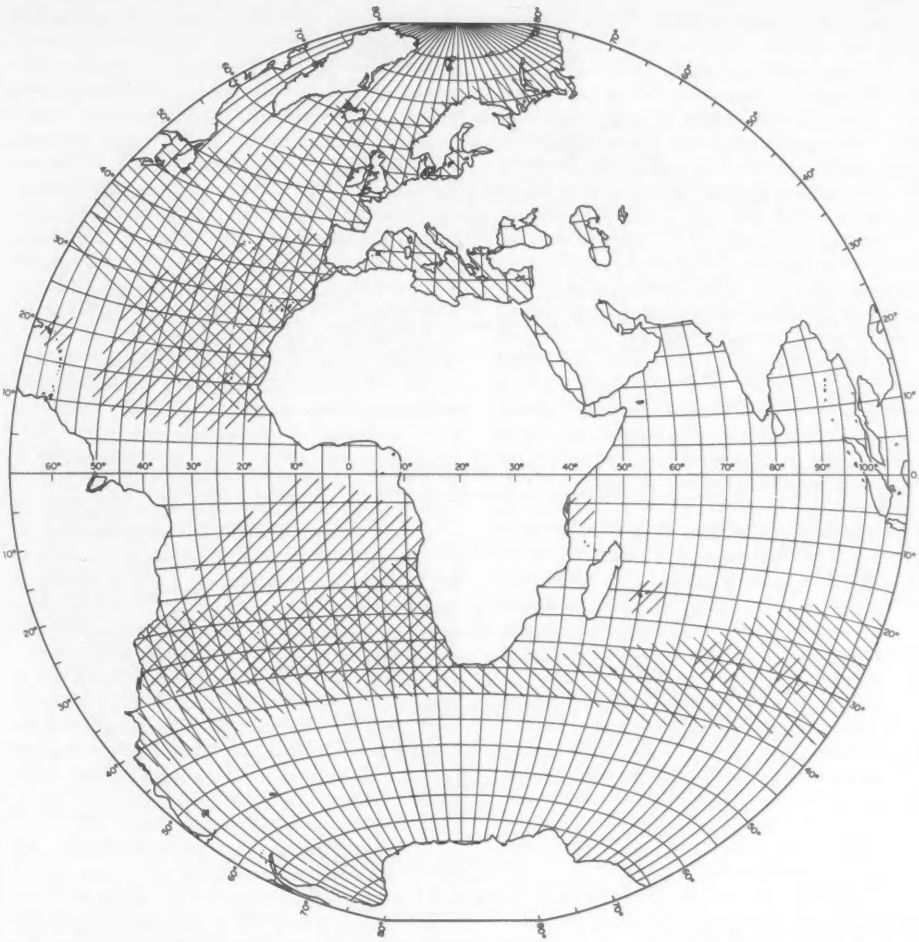

FIGURE 16.—Overlapping distributions of Scomberesocidae in the Eastern Hemisphere. Lines sloping downward to the left refer to *Nanichthys simulans*; lines sloping downward to the right refer to *Scomberesox saurus* in the Atlantic and Indian Oceans.

"young" specimens could have been confused. Mann (1954b, 1960) listed no scomberesocids or beloniforms from the Patagonian area. Also, there appears to be confusion as to the locality of the capture stated by Lönnberg: Smyth Channel and Eden Harbor appear to be about 240 mi apart. According to Defense Mapping Agency Chart 22ACO 22390, Eden Harbor (now Puerto Eden) lies on a narrow channel along the east side of Isla Wellington, about 49°09′ S, 74°24′ W. This is far inland from the open sea and is a seemingly improbable place to find a synentognath fish. Smyth Channel (Defense Mapping Agency Chart 22XHA 22404) opens to the Pacific Ocean at about 52°50′ S, 73°50′ W (about the center of its wide mouth) and extends northerly to about 52°23′ S, where it merges with Mayne and Gray Channels. If scomberesocid fishes of any size occur in the area, the mouth of Smyth Channel is a more probable place than the inland Eden Harbor. The taking of seven young of *S. s. scombroides* at 47° S, 81° W, cited above, lends some credence to the possibility of the

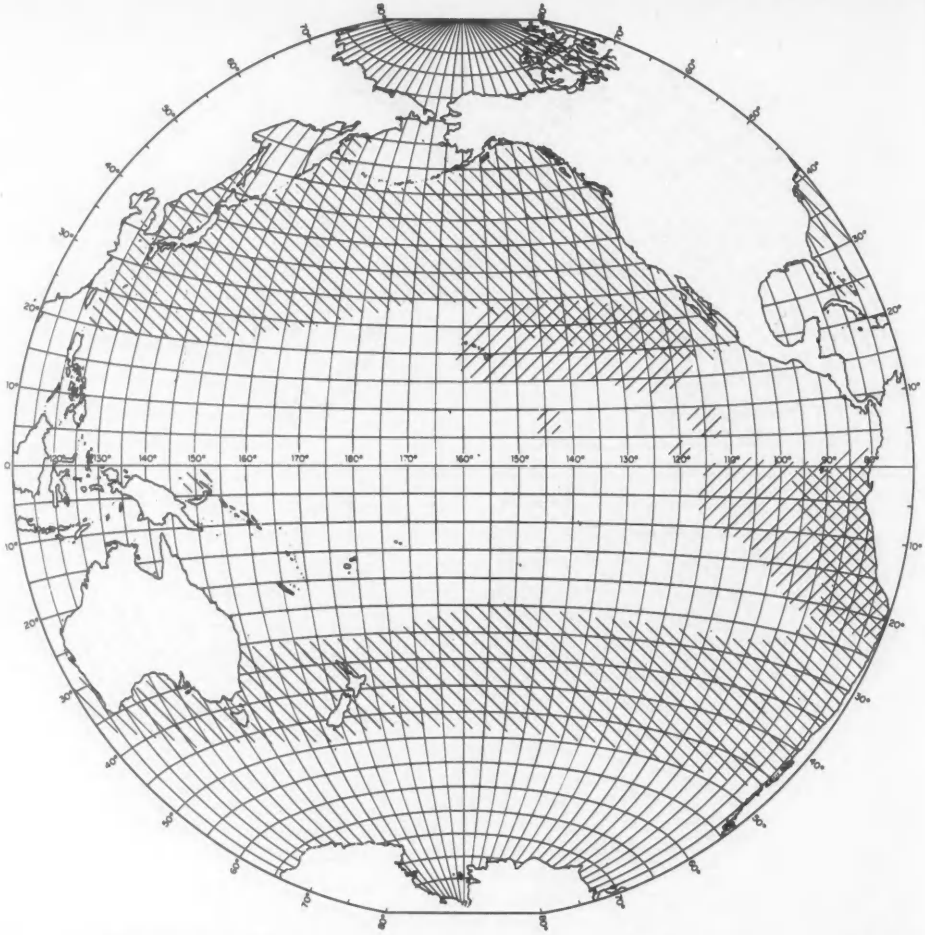

FIGURE 17.—Overlapping distributions of Scomberesocidae in the Western Hemisphere. Lines sloping downward to the right refer to *Cololabis saira* in the North Pacific and near New Guinea, and to *Scomberesox* ssp. in the South Pacific and extreme northwestern Atlantic; lines sloping downward to the left refer to *Elassichthys adocetus*.

species being taken in the wide oceanic mouth of Smyth Channel some 400 mi farther south.

Our findings on the distribution of *S. s. scombroides* westward across the South Pacific differ little from that shown by Parin (1968a).

The northern subspecies, *S. s. saurus*, occurs widely in the North Atlantic Ocean, north of about 30° N, but rather sparsely in the central area, where it is very largely replaced by *Nanichthys* (Figures 12, 14, 16). It ranges along North America from Florida (rarely) to Newfoundland, and well into the Gulf of St. Lawrence (Vladykov and McAllister 1961) and to Iceland (Saemundsson 1949). The species occurs uncommonly along the eastern shores of the United States south of New Jersey. It occurs at the oceanic islands of the eastern North Atlantic, throughout the Mediterranean, Aegean, and Adriatic Seas, the British Isles, and along Norway to near Nordkapp. It has been reported from the Barents Sea, and from the

White Sea in Kandalaksha Bay, about 67° N, 32°45′ E (Andriashev 1954, after Novikov). Berg (1939) reported it from the western entrance to the Strait of Matochkin Shar, Novaya Zemlya Island (about 73°16′ N, 56°27′ E); Andriashev (1954) gave the length of this specimen as 25 cm. Presumably the species is rare that far north and is a summer migrant. However, it has been reported (Anonymous 1970) that four Russian vessels captured 7 to 10 metric tons per vessel per day of "saury" in late September 1969 near Novaya Zemlya. W. L. Klawe[16] feels that these large catches of *Scomberesox* so far north actually represented either "saida" (*Pollachius virens*, the Atlantic pollock) or "saika" (*Boreogadus saida*, the Arctic cod), and that the use of the Russian vernacular "saira" (= saury) was either a misprint or misinterpretation.

The southern extension of *S. s. saurus* into the central North Atlantic, to 15° N (Figure 14) is probably due to the southeasterly flowing currents of the huge gyre that extends across the ocean between about 40° and 20° N; the southern border of this gyre forms the northern boundary of the west-flowing North Equatorial Current; its southerly boundary reaches to about 5° N.

Nanichthys is common in the more central parts of the North and South Atlantic Ocean but is not common in the Indian Ocean (Figure 12). We enter on the distributional chart (Figure 12) a question mark in the Red Sea on the dubious basis of Borodin's (1930) record of "*Scomberesox saurus*, young" from the "Red Sea" (accepted by Fowler 1956). The record is questioned because Borodin's identifications have proved to be commonly inaccurate, and we have not seen the specimen (which has been reported to us as no longer extant in the Vanderbilt Museum). If the record was not based on a juvenile hemiramphid or other nonscomberesocid synentognath, it may have been based on *Nanichthys*, which we have seen from Zanzibar. We also enter a question mark (Figure 12) in reference to the record of *S. saurus* reported by J. L. B. Smith (1955). Smith[17] has stated: "With regard to the Aldabra record, I regret that we cannot find the specimen. In our field notes this species is entered as 'Juvs. in stomach of Tunny.' Neither my wife nor I can remember whether that material was kept or not; it probably was in a bad state."

The records of capture of *Nanichthys* in the Indian Ocean are too few to warrant more than conjecture as to limits of distribution there; it is either uncommon or has been very infrequently taken. No specimens resulted from the broad station coverage of the International Indian Ocean Expedition, 1963-64. N. V. Parin[18] did not encounter any specimens of *Nanichthys*, although he did report many captures of *S. s. scombroides* (Figure 14). Sauvage (1891) listed "*Scombresox saurus*" from near Madagascar, within a rather broad area bounded by "3^{E} et 26^{E} parallèles et les 42^{E} et 65^{E} méridiens." Misidentification is possible as Sauvage included species of Belonidae, Hemiramphidae, and Exocoetidae in his "Scombresocidae"; no size or number of specimens was given.

In most of the records of *Nanichthys* from the North Atlantic Ocean, the greatest number of captures lie within the large eddy system and easterly of about 40° W, extending to the African coast. The southern border of the range, ca. 10° N, is at about the middle of the North Equatorial Current, and the northern border, at ca. 35° N, at the northern margin of the eddy and the southern margin of the Gulf Stream and of its continuation—the North Atlantic Current. There is little difference in current structure between winter and summer in the southern portion of the North Atlantic (Anonymous 1965), and the currents are relatively slow during both periods. Oddly, *Nanichthys* is infrequently taken west of about 40° W, the most westerly occurrence being near St. Thomas Island, West Indies (Figure 12). *Nanichthys* appears to be more antitropical in distribution than does *Elassichthys*. Ueyanagi et al. (1972) mapped the occurrence of a juvenile at about 02° S, 10° W (Figure 12).

In the Atlantic, in both hemispheres, this dwarfed form has often been confused by authors with the young of *Scomberesox*. The material reported by Murray and Hjort (1912) ("M" in Figures 12 and 14), and by Lütken (1880) from the North Atlantic in part represent *Nanichthys*. Each author stated that the young of *Scomberesox* were taken in great numbers in collections from the open Atlantic; each figured (as young of *Scomberesox saurus*) the distinctive beak structure of

[16]W. L. Klawe, Inter-American Tropical Tuna Commission, La Jolla, Calif., pers. commun. 20 March 1970.

[17]J. L. B. Smith, Department of Ichthyology, Rhodes University, Grahamstown, South Africa, pers. commun. 20 November 1964.

[18]N. V. Parin, P. P. Shirshov Institute of Oceanology, Akademia 117218 Moscow, Krasikowa 23, U.S.S.R., pers. commun. 14 September 1978.

adult or semiadult *Nanichthys*—the upper beak notably shorter than the lower. We have examined most, if not all, of these specimens and found them to be referable to *Nanichthys*. Also, most of the reports of *Scomberesox saurus* from the South Atlantic and Indian Oceans by Lampe (1914) ("L" in Figure 12) may, on the basis of geographical evidence, be referable to *Nanichthys*. We have, however, not seen the specimens, but many of Lampe's collections occurred in the area of overlap (Figure 16). Dudnik (1975a) reported on an extensive collection of "*Scomberesox saurus*" from the South Atlantic (about 3,000 specimens, from 8 to 460 cm). In general his data agree well with ours and with Parin's (1968a, b) but he shows (Dudnik 1975a, fig. 2) the species to extend northward to about 18° S along the coast of Africa. This is notably farther north of the expected range but is well within that of *Nanichthys*. He did not discuss the dwarf ("*Scomberesox* sp") in his study (Dudnik 1975a), submitted for publication on 20 January 1974, nor did he compare it with its larger relative, although presumably he was aware of the form and of Parin's (1968a) study for he submitted his own (Dudnik 1975b) concerning it on 20 November 1974. As no tabular or descriptive morphological data were offered in the first study (on *Scomberesox saurus*), it is not entirely clear whether or not Dudnik (1975a) dealt only with the larger form, for he indicated that only smaller specimens, larvae to juveniles up to 100 mm (a size range encompassing most adults of *Nanichthys*), occurred north of 20° S. Also, in his later work on *Scomberesox* sp. (= *Nanichthys simulans*), Dudnik (1975b) showed collections of the dwarfed form between about 10° and 15° S in this same area off Africa.

The dwarfed form, *Elassichthys adocetus*, of the eastern Pacific Ocean also has been confused with the young of *Cololabis saira*. Roedel (1953) and Chirichigno F. (1962) reported *C. saira* (as young) from off northern Perú. Schaefer and Reintjes (1950) reported (as young of *C. saira*) specimens of *E. adocetus* from between the Hawaiian Islands and the western coast of North America.

Elassichthys adocetus appears to be less antitropically distributed than is *Nanichthys simulans* in the Atlantic Ocean. A few specimens have been taken between the two principal areas of occurrence north and south of the Equator (Figure 13); perhaps these are strays from the main groups (presumably from the southern) and transported there by the complex current systems of the area and/or associated with oceanic fronts, as reported by Knauss (1957) in the vicinity of 03° N, 120° W.

An interesting aspect of the distributions of the northern population of *E. adocetus* is its absence from the large area bounded by about 115° W and the Equator. Also, it has not been taken within hundreds of miles of the coast of Baja California, México. In contrast, the species is very common in the coastal waters of Ecuador and Perú. One reason for the avoidance (or absence) of the area westerly of Baja California may be the still cool water of the California Current, between 18° and 25° N. This broad current is evident out to about 120° W and flows southerly to about 22° N between January and June-July before turning westerly and mixing with the North Equatorial Current; from August to December these two currents merge at or north of 20° N. Temperatures within this large area range between 25° and 29° C (Wyrtki 1964) and are probably above the optimum tolerated by the species. Also, this area is one of very low oxygen content (0.05 ml/l), but this may not be a factor in the distribution of *E. adocetus* as it is an entirely surface form and probably remains well above the upper depth limit of the O_2 minimum layer, between 50 and 200 m (Wyrtki 1967).

The occurrence of *E. adocetus* (and *S. saurus scombroides*) near the coasts of Ecuador and Perú, and its westward extension of range to about 115° W near the Equator, are no doubt due to the still cool water of the Perú Current; the temperatures range to about 20°-26° C in summer and 16°-24° C in winter, between about 0° and 22° S (Wyrtki 1964).

In the northeastern Pacific Ocean the ranges of *C. saira* (again mostly juveniles and young) and the northern population of *E. adocetus* overlap in an extensive area roughly bounded by about 20° to 30° N, 115° to 155° W (Figure 17); perhaps the overlap is primarily seasonal but often the two have been taken together in the northern portion of the overlap area. King and Iversen (1962:320, app. table 8) reported one specimen (86 mm) of "Scomberesocidae" from the Equatorial Counter Current (ECC) in 1955-56. No coordinates were given but the collection was made between about 108° and 160° W within the ECC, the boundaries of which these authors indicated to be between about 5° and 10° N (p. 286, fig. 12). The stated size ("86 mm") is notably longer than the largest of hundreds examined by us (about 68 mm SL), but it can scarcely be other than *Elassichthys*, which is

common within the ECC. The southernmost known occurrence of *C. saira* is some hundreds of miles to the north.

Cololabis saira apparently does not occur south of about 20° N (Figure 15), based on our data and those of Parin (1960). North of this latitude it ranges throughout the North Pacific to the Aleutian chain, but apparently not into the eastern and central Bering Sea. In the far western area it occurs in the eastern portion of the Yellow Sea, the entire Sea of Japan to well along Sakhalin, into the southern Okhotsk Sea, and northerly along the Bering Sea coast of Kamchatka to Olyutorsky Bay, at about 60° N (Parin 1968a, b) (Figure 17). Along the North American coast *C. saira* is very common from Alaska to at least central California, but only sporadically so to about the Cedros Island region of Baja California, México; it is relatively uncommon south of that region, particularly adults, but young and juveniles have been taken at about 19° N in the eastern Pacific.

Cololabis saira juveniles (8-30 mm) were reported from 180 mi east of Port Macquarie (New South Wales, Australia) by Fourmanoir (1971); however, we have examined these small fishes and determined them to be *S. s. scombroides*. One apparently valid capture of *C. saira* near New Guinea (kindly communicated to us by N. V. Parin, 14 September 1978) was reported by Kailola (1974): ". . . one specimen. East of Kavieng [New Ireland] (2°34′ S, 150°49′ E) Dipnetted by night light, 1967.—205 mm SL." The count of dorsal and anal finlets (5 each) indicates the specimen is a scomberesocid, and certain proportions listed can pertain only to *Cololabis*: "Eye 5, 1.8 in snout. Snout 2.7 in head," falling far outside the range for *Scomberesox* of similar size. The stated size, 205 mm, is far too large for *Elassichthys*. This locality (Figure 15, large hexagon) is about 1,800 miles south of any other known occurrence of *C. saira* in the western Pacific. Parin believes, and we concur, that this specimen was very probably lost from a Japanese longline vessel; Fourmanoir and Laboute (1976) describe the use of frozen sauries (*C. saira*) as bait by longliners operating in the area.

Intriguing questions arise concerning this apparently valid capture in the Southern Hemisphere. We assume that the specimen was alive (at least it was not stated otherwise). Kailola (1974) postulated that "abnormal extensions of cold currents south of the Equator may thus account for the southern record of the species." An alternative explanation is that the specimen was transported alive from northern waters in a bait tank aboard a vessel. However, *C. saira* does not keep well in live-bait tanks; they are "wild" and dash themselves to death against the walls, particularly of small tanks. And, to our knowledge, there are no recorded instances of a Japanese longline vessel carrying large live-bait tanks.

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ADDENDUM

Fossil Fishes from California Referred to Scomberesocidae

We are uncertain of the synonymic status of the nominal genus *Scomberessus*, based on a fossil from the Miocene (Monterey) formations, introduced by Jordan (1920). By context, Jordan proposed *Scomberessus* as a new genus, as follows: "**Scomberessus** Jordan, 571 [referring to the same item in *The Genera of Fishes*], orthotype SCOMBERESOX ACUTILLUS J. & G. (fossil). Differs from the living genus SCOMBERESOX in the much larger dorsal, of 16 rays." But an examination of the text and figures of the two fossil specimens described by Jordan and Gilbert (1919: 37-38, pl. XIV, fig. 2, and XVIII—*Scomberesox acutillus* and *S. edwardsi*) indicate a serious confusion. The one item of diagnosis (dorsal fin) was obviously drawn not from the account and figure of *Scomberesox acutillus* Jordan and Gilbert (1919:37-38, pl. XIV, fig. 2 [the paratype]), but from the description and figure of *Forfex hypuralis* Jordan and Gilbert (1919:36-37, pl. XIV, fig. 3). The description of *S. acutillus* states only "dorsal obliterated," also, the paratype (a complete skeleton examined by us) shows no remaining trace of a dorsal fin. The description of *F. hypuralis* lists the dorsal rays as "apparently I, 16 in number" and the figure shows a long-based dorsal of approximately the stated number of rays and beginning before the middle of the body (without head). The juxtaposition of the two figures on the plate presumably led the aged master astray. Despite the nonapplicability of the one stated character, the generic name *Scomberessus* must, we assume, rest on the designated type-species, *Scomberesox acutillus*.

Regardless, we are more concerned with the reference of these fossils to the family Scomberesocidae. We have examined the paratype of *Scomberesox acutillus* (a complete skeleton but with crushed head), and five essentially complete skeletons referable (presumably) to *S. edwardsi* (the holotype is a head and anterior few vertebrae) and have failed to find any finlets—a key character of the family—this despite the listing by Jordan and Gilbert (1919) of ". . . traces of five finlets" for *S. acutillus* (the paratype); under high magnification these traces proved to be isolated scales.

David (1943) may have inferred the presence of finlets by listing counts for *S. edwardsi* of "Dorsal fin 14, V; anal fin 18, VI . . . ." As Roman numerals have long been used to designate spiny or unsegmented rays, and as living scomberesocids and related fishes all have segmented rays, we assume that David was referring to finlets. However, on examination of David's and other material labelled *S. edwardsi*, we find nothing to substantiate a count including any "V" or "VI," particularly for finlets.

Each finlet of the Scomberesocidae and Scombridae (mackerels and tunas) arises from a single base (ray) that branches into a fanlike structure that is much more robust than a slender, single ray of the dorsal and anal fins proper. Since the individual rays of these fins are distinctly evident on some of these fossils, it is reasonable to expect the heavier finlets also to be preserved or that an imprint at least would have remained.

The lack of imprint of finlets is substantiated by the absence of any (or imprint) of the supporting bones associated with them. In present scomberesocids these supporting bones are robust, flattened laterally, and lie embedded somewhat parallel to the surfaces of the caudal peduncle rather than extending more or less vertically between the neural and haemal spines, as do those of the rays of the main portions of the fins. Thus, since the supporting rays of the main portions of the fins are often visible in the fossils, it is reasonable to expect such rays of the finlets also to be visible, if present.

In addition to the apparent lack of finlets on these fossils (labeled as of Clarendonian stage), there are notable differences in proportions in lengths of anal bases and caudal peduncle between them and present *Scomberesox*. In two fossils on which the anal fins appear to be entire (none have complete dorsal fins) the length of this fin is slightly shorter than the length of caudal peduncle (23.7 vs. 26.5 and 28.5 vs. 33.2 mm). In present *Scomberesox* the caudal peduncle is about 2.5 times the length of either the dorsal or anal fin base, exclusive of finlets. In this regard the fossils approach the condition found in the Belonidae, wherein the length of the caudal peduncle is one-half or less as long as the fin bases; in *Ablennes hians* the peduncle is scarcely more than one-fourth the length of these bases. Thus, among known marine fishes with both jaws greatly prolonged into beaks, these fossils are about midway between present belonids and *Scomberesox* in the ratio of lengths of caudal peduncle to the base of either dorsal or anal fins (exclusive of finlets in the latter group). An additional difference is a notable

reduction in numbers of vertebrae in those fossils with complete skeletons, 54-58 vs. 64-70 in present *Scomberesox*, and 62-69 in *Cololabis*.

Due to the apparent absence of finlets and the discrepancy in lengths of caudal peduncle and anal fin base, and the many fewer vertebrae, it seems justifiable to remove these fossils from the family Scomberesocidae. To retain them therein would require acceptance of development of finlets and drastic modification of the peduncular region since the Miocene period (7-26 million years BP [Before Present]) and a gain of at least six vertebrae; we hold these to be improbable occurrences. In any event, the name *Scomberessus* appears to have no bearing on the new generic names proposed herein.

Furthermore, we find no sound basis for even the doubtful reference of *Praescomberesox pacificus* David (1946:58-59, pl. 2, fig. 3, and pl. 3, fig. 2) to the Scomberesocidae on the basis of isolated scales found in a core from oil-well drilling at a depth between 3,895 and 3,907 feet (holotype).

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EFFECTS OF TEMPERATURE AND SALINITY ON PRODUCTION AND HATCHING OF DORMANT EGGS OF *ACARTIA CALIFORNIENSIS* (COPEPODA) IN AN OREGON ESTUARY

JOHN KENNETH JOHNSON[1]

ABSTRACT

Experimental results indicate that induction of dormancy in *Acartia californiensis* eggs is temperature dependent and occurs below 15° C in two ways: 1) Cold adapted females spawn true resting eggs which exhibit major differences in hatching and survival rates from nondormant eggs under similar conditions. 2) Nondormant eggs spawned above 15° C may become dormant and have short-term viability at temperatures below 15° C. Salinity does not induce dormancy.

Hatching results of field-collected resting eggs at naturally occurring temperature-salinity combinations demonstrate that termination of dormancy is also primarily temperature dependent. Salinity, however, regulates rate and success of hatching. In addition, heavy naupliar mortality occurs following hatching at low salinities. Substantial hatching must occur in the field over much of the year. Since subsequent survival and population growth depends on the presence of favorable temperature and salinity conditions, nauplii which hatch during the low salinity winter and spring months in Yaquina Bay must be lost. This phenomenon is viewed as a "leaky" population diapause.

Resting eggs were also demonstrated for *Epilabidocera longipedata* and *Eurytemora affinis*, an occurrence previously undescribed in the literature.

Resting eggs have been known to be a common adaptation in freshwater zooplankton since the turn of the century (see reviews in Hutchinson 1967 and Elgmork 1967). The existence of a comparable resting egg phase in the life cycle of marine neritic species was postulated for many years to explain the seasonal disappearance of coastal species from the water column (e.g., Fish and Johnson 1937; Barlow 1955; Conover 1956). Preliminary evidence of marine calanoid resting eggs was first reported by Sazhina (1968) for the species *Pontella mediterranea* and *Centropages ponticus*.

Zillioux and Gonzalez (1972) conclusively demonstrated with laboratory and field evidence that the seasonal disappearance of *Acartia tonsa*, a common coastal species, coincides with the production of overwintering eggs as water temperatures fall below 14.5° C. Subsequent research has shown that egg dormancy is an important adaptation in many boreal and temperate neritic calanoids, including both summer-fall species (e.g., *Tortanus forcipatus*, Kasahara, Onbé, and Kamigaki 1975; *Labidocera aestiva*, Grice and Gibson 1975) and winter-spring species (e.g., *A. clausi*, Uye and Fleminger 1976; *C. abdominalis*, Pertzova 1974). Egg dormancy probably enables most coastal species to survive periods during which conditions in the water are unfavorable.

Environmental factors such as temperature or photoperiod usually govern the induction of dormancy in arthropods (Lees 1955). Both the adult and/or the egg may be responsive to adverse environmental changes. Egg dormancy may result from a physiological response of the female to a changing milieu which modifies the eggs. Conversely, dormancy may develop as a response of the egg to changes in conditions as it sinks through the water column into the bottom sediments. There is evidence for both mechanisms in marine copepods. Zillioux and Gonzalez (1972) demonstrated that the production of resting eggs by *A. tonsa* is a response of the female to low temperatures. However, Uye and Fleminger (1976) examined egg development of four *Acartia* species (including *A. tonsa*) from southern California waters at various temperature and salinity combinations and concluded that dormancy is primarily a response of the egg to the milieu. Their results led them to hypothesize that exposure of the eggs to abnormal salinities may be necessary to induce dormancy in at least two of the species of *Acartia*. Once buried in the sediments,

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egg dormancy is maintained by low oxygen levels (Kasahara, Onbé, and Kamigaki 1975; Uye and Fleminger 1976). Light is also required to break dormancy in at least one species, *A. clausi* (Landry 1975a; Uye and Fleminger 1976).

Further work is required to fully demonstrate the factors regulating dormancy in coastal calanoids. A localized summer-fall population of *A. californiensis* in Yaquina Bay, Oreg., affords an excellent opportunity to examine this phenomenon, since the entire winter-spring period is passed in the resting egg stage. A field research program provided data for the correlation of population dynamics with temperature and salinity. Laboratory experiments were carried out to determine the relative importance of temperature and salinity in the formation and subsequent hatching of dormant eggs of *A. californiensis*. Analysis of the data provides additional information on the role of the female versus that of the egg in development of dormancy.

Acartia californiensis, a newly described species (Trinast 1976), is useful for comparative studies in egg dormancy since it displays close affinities to *A. tonsa* in both physiological and morphological features. Earlier studies in Yaquina Bay (Zimmerman 1972; Frolander et al. 1973; Johnson and Miller 1974; Miller et al. 1977) identified the species as *A. tonsa* in the belief that it represented a smaller, ecophenotypic variant of the larger, offshore, *A. tonsa* present in the northerly Davidson Current during the winter months. Furthermore, the unidentified "*Acartia* sp. I" discussed by Uye and Fleminger (1976) has been recently identified as *A. californiensis* Trinast by A. Fleminger,[2] thus permitting comparison of egg dormancy in northern and southern populations.

METHODS

The seasonal population cycle of *A. californiensis* in Yaquina Bay was determined by the collection of plankton samples twice weekly at Stations 21, 29, 39, 45, and 57 (Figure 1). Sampling was done from June to November in 1972-74 with a Clark-Bumpus sampler (mouth diameter 12.5 cm) fitted with a 112 μm mesh net which quantita-

[2]Abraham Fleminger, Scripps Institution of Oceanography, University of California, La Jolla, CA 92037, pers. commun. June 1978.

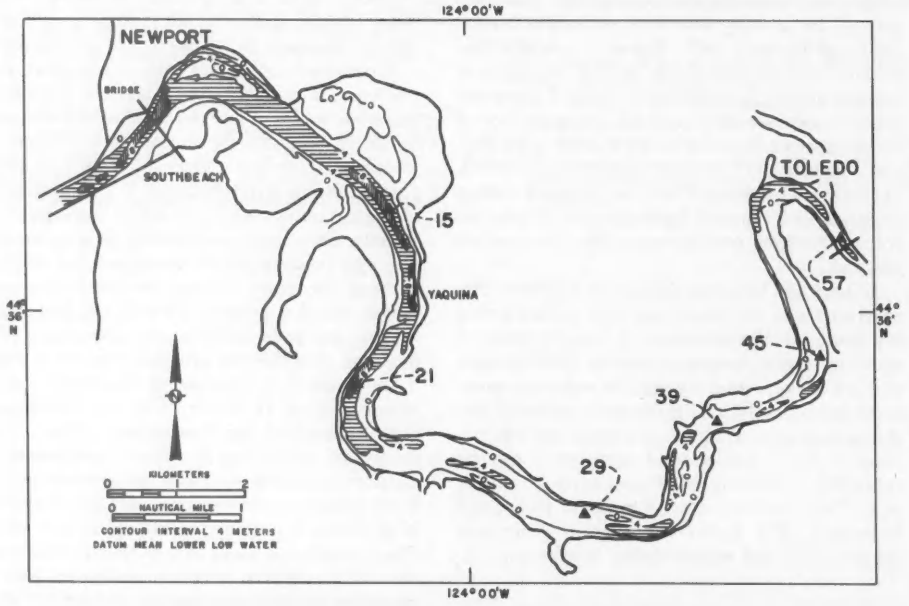

FIGURE 1.—Sampling stations for *Acartia californiensis* in Yaquina Bay estuary, Oreg.

tively retained all copepodite stages. Tows were oblique in a stepwise pattern from just above the bottom to near surface at midchannel. A calibrated propeller flowmeter in the mouth of the net was used to estimate the quantity of water filtered. Volumes filtered were typically 5-6 m^3. Temperature measurements and salinity samples were taken at the surface and just above the bottom at each station. Salinities were later determined by inductive salinometer in the laboratory.

RESTING EGG PRODUCTION

October Experiment

Adult *A. californiensis* were collected at Station 39 (Figure 1) on 9 October 1975, using a 239 μm mesh net towed slowly at 1-2 m depth. Surface temperature and salinity were 14.9° C and 26.8‰, respectively. Laboratory cultures were established the same day by sorting 50 female and 25 male adults into each of eight 1,400 ml beakers containing 1,200 ml of Millipore[3]-filtered water (25‰). Water temperature increased to room temperature (16.8° C±0.3°) during this time. Upon completion of sorting, all newly spawned eggs were removed by screening and discarded. Replicate cultures were then transferred to water baths and maintained at 21°, 17°, 13°, and 9° C (±0.1°). Continuous overhead lighting (low level) was used throughout the experiment.

Adults were fed daily with a mixture of *Pseudoisochrysis* sp., *Isochrysis galbana*, and *Thalassiosira fluviatilis* at a concentration of approximately 200,000-250,000 cells • ml^{-1}. Phytoplankton cultures were maintained in log-phase at 16.8° C. Viability of the algal species over the temperature range of 9°-21° C was not determined but assumed to be unimportant in the experimental design since *A. californiensis* adults were provided excess food daily. In addition, adult mortality was moderately low (estimated at <20%) during the acclimation and spawning period with similar losses observed in all cultures. Thus, selection of adults in response to temperature or food during the acclimation period was not likely a factor in influencing the type of egg spawned.

After the third day of adult acclimation, accumulated eggs were removed by gentle screening. The eggs were used in a preliminary experiment on hatching success which differed from the main experiment in that fewer hatching temperatures were tested for eggs produced at each acclimation temperature.

The main experiment was established with eggs collected on the eighth day of adult acclimation. Maximum egg age ranged from 5 days at 9° C to 1 day at 21° C because of differences in egg development rate as a function of temperature. Eggs from replicate cultures at a given acclimation temperature were mixed together in a Petri dish for sorting by pipette. Water temperature was maintained as close as possible to acclimation temperature during sorting. Depending on the number of eggs available, 10-15 replicate batches of 50 eggs each were placed in small 6 ml Petri dishes (1 cm depth, 3.5 cm in diameter) containing 4-5 ml of Millipore-filtered water (25‰). Dish bottoms were marked in a grid for ease in counting at 25× with a dissecting scope. Salinity changes caused by evaporation were prevented by floating the small dishes in transparent, tightly capped 100 ml beakers filled with 80 ml of water (also 25‰). Two and usually three or more replicate dishes of 50 eggs were then placed in each of five water baths at 21°, 17°, 13°, 9°, and 5° C, respectively. This procedure was repeated for eggs produced at all four acclimation temperatures (21°, 17°, 13°, 9° C), resulting in an experimental design (Table 1) using over 2,500 eggs.

Hatching success was determined daily by making separate counts of eggs remaining and hatched nauplii. Nauplii were captured and removed daily with a pipette. Every 5th day, water was changed by pipette with minimum disturbance to the remaining eggs. Unhatched eggs were maintained at the experimental temperature well past the time expected for normal hatching (Table 2) and then transferred to a favorable temperature (21° C) to determine subsequent hatching success.

November Experiment

Animals collected on 4 November 1975 at Station 39 (12° C, 21‰) were used to repeat the experiment at the prevailing field temperature and salinity conditions. By this time, the field population of *A. californiensis* was greatly reduced and egg production was assumed to be primarily resting eggs. Females were kept at 12° C and 21‰ during transfer to the laboratory and subsequent culturing. Eggs were collected on the fourth day of

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Production of resting eggs and summer eggs by female *Acartia californiensis* collected for the October experiment, 9 October 1975. Hatching results at each temperature-salinity combination expressed as a mean percentage for two and usually three replicates of 50 eggs each.

Cumulative time (days)	Event		Conditions																					
0	Collection		14.9° C, 26.9‰; Station 39, Yaquina Bay, Oreg.																					
0-1	Preliminary acclimation		14.9° C, 25‰; (temperature increasing to 16.8° C)																					
	Spawning:		21° C					17° C					13° C										9° C	
5-9	Main experiment		25‰					29‰					25‰										25‰	
	Adjusted time	Hatching temp (° C)	21°	17°	13°	9°	5°	21°	17°	13°	9°	5°	21°	17°	13°	9°	5°	21°	17°	13°	9°	5°	13°	9°	5°
9	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	1		92	84	70	5	3	98	93	39	8	2	12	7	1		0	0	30	1		0	0	0	0
11	2		96	100	79	12	6	99	99	63	17	2	18	11	3	1	0	0	42	25		0	0	0	0
12	3	Results in cumulative	97		89	23	8	99	100	66	25	4	42	15	4	1	0	0	53	27		0	2	0	0
13	4	percentage hatched	97		90	26	8	99		67	28	5	65	21	4	1	0	0	65	29		0	2	0	0
14	5		97		90	32	9	99		67	31	5	73	32	4	1	0	0	72	31		0	3	0	0
17	8				90	34	9			71	34	5	91	54	4	1	0	0	82	47		0	3	0	0
20	11				90	35	9			71	35	5	97	76	4	1	0	0	89	64		0	3	0	0
24	15					35	9				35	5	97	92		1	0	0	89	79		0		0	0
29	20						9					5	97	99			0	0	89	87				0	0
129	120						9					5					0	0						0	0
		Warming (21° C) on day			11	15	120			11	15	120			11	15	120				11	15	120	
		Subsequent hatch (%)			0	39	0			19	61	0			91	96	30				76	81	71	
		Final hatch (%)	97	100	90	74	9	99	100	90	96	5	97	99	95	97	30	89	87	79	81	71		

spawning at 12° C and sorted into replicate batches of 50 eggs each. Hatching rate and success were determined at 21°, 17°, 15°, 13°, 9°, and 5° C in 25‰ water. Other procedures were as described above.

TABLE 2.—Nondormant egg development time for *Acartia tonsa* and *A. clausi* as a function of temperature, and time that unhatched eggs of *A. californiensis* were initially held at the same experimental hatching temperature (October experiment).

Temp (° C)	Egg duration (days)		Incubation time (days)	
	A. tonsa[1]	*A. clausi*[2]	*A. californiensis* 21°-17° C[3]	*A. californiensis* 13°-9° C
21	1.3	1.2	5	20
17	1.9	1.5	3	20
13	3.1	2.2	11	11
9	8.5	3.8	15	15
5	45.1		120	120

[1]Data based on prediction of Bělehrádek function (Zillioux and Gonzalez 1972).
[2]Data from experimental observations of Landry (1975b).
[3]Temperatures at which *A. californiensis* eggs were spawned.

HATCHING OF RESTING EGGS COLLECTED IN THE FIELD

A series of preliminary experiments (J. K. Johnson, unpubl. data) had demonstrated that resting eggs of *A. californiensis* and *A. clausi* occur in similar numbers in the surface sediments in the vicinity of Station 39 (Figure 1). Unfortunately, the resting eggs of the two species are not distinguishable from each other on the basis of diameter, shape, or color. Therefore, the following hatching experiments include resting eggs of both species at unknown ratios. Much information and insight were gained in spite of this serious experimental limitation.

Salinity Experiment

Resting eggs were obtained by collecting mud with an Eckman-Birge grab 500 m upstream of Station 39 on 7 February 1976 during low tide. The upper 1-2 cm of sediments were saved for later screening. Temperature and salinity values near the bottom were 9.8° C and 4.1‰. An accompanying series of plankton tows from Station 21 to Station 45 verified that no copepodite stages of *A. californiensis* were present in the upper estuary, as expected from earlier field work. *Acartia clausi* was present in low numbers only at Stations 21 and 29 ($<50 \cdot m^{-3}$). It does occur at Station 39 during January to April but only at extremely low densities (ca. $5\text{-}20 \cdot m^{-3}$) during periods of high tides (Zimmerman 1972). Thus, few recently spawned eggs were likely to be present in the sediments collected at Station 39.

Sediment samples were maintained at field temperature (10° C) during transport to the

laboratory and storage in the dark for 1 mo. Resting eggs were removed (10 March 1976) by first sieving the sediments through 119 μm and 64 μm mesh nylon screens. This size fraction was diluted with water (5‰), stirred well, and allowed to settle. Approximately 5-6 ml of the surface sediments were then slowly introduced by pipette onto the surface of 8-10 ml of a 2.8 M aqueous sucrose solution (suggested by Brewer 1964) in each of several 15 ml centrifuge tubes. Following centrifugation at 1,000-2,000 rpm for 1-2 min, resting eggs of *Acartia* spp. and other species (including calanoids, harpacticoids, and rotifers) were removed by pipette from the water-sucrose interface. These eggs were nearly free of detritus. A thorough rinse with Millipore-filtered water (5‰) on a 64 μm mesh screen removed the sucrose solution. No evidence of egg distortion or crushing was found to result from the high osmotic gradient. In contrast, eggs centrifuged from surface sediments collected in September collapsed under similar conditions.

Following rinsing, *Acartia* spp. eggs were sorted from extraneous material and then mixed in a Petri dish in 5‰ water. Approximately 2,000-2,500 eggs were collected in 3-4 h of work. Most eggs had a clear, outer layer which surrounded a dark inner mass, similar to that reported for resting eggs of *Labidocera aestiva* (Grice and Gibson 1975). A moderate number of eggs (ca. 10-20%), lacking the clear layer, had ended diapause and progressed to various stages of embryogenesis. These latter eggs were most likely undergoing development in the uppermost sediment layer when collected in February. Only those eggs with a clear outer layer were used for the experiment.

Thirty-five resting eggs were sorted by pipette into each of 43 small (6 ml) Petri dishes. The accompanying water at 5‰ (ca. 1 ml) was removed by pipette. Water of 11 salinities, ranging from 0‰ (glass distilled) to 23.5‰, was then added to batches of three or more of these dishes. Three complete rinses of appropriate salinity were added and removed before the final addition. The Petri dishes with eggs were maintained at 17° C (±0.1°) in covered beakers as described above. Continuous overhead lighting was provided. Water was replaced every 5th day.

Egg and naupliar counts were usually made daily. There were some 2-day intervals. Naupliar mortality between observations was also recorded. Salinity was increased in some replicates at various time intervals to determine viability of remaining dormant eggs. Hatched nauplii were captured and reared to copepodite stages (17° C, 20‰) for positive species identification because of uncertainty in distinguishing between *A. californiensis* and *A. clausi* nauplii.

Salinity and Temperature Experiment

The effect of salinity on hatching of resting eggs was later evaluated at three more temperatures (15°, 12.5°, 10° C) to obtain hatching rates at temperature-salinity combinations normally present in the upper estuary during later fall and early spring months. Resting eggs were obtained by 2.8 M sucrose centrifugation of sediments collected at Station 39 on 18 February 1978. Water conditions were 9.4° C and 7.6‰. Transport to the laboratory, storage (2 days), screening, centrifuging, and sorting were all done at 10° C. Two or three replicates of 35 resting eggs (clear-layer type) were prepared at 5‰, 10‰, 15‰, and 25‰ for each temperature. Other details were as described in the salinity experiment.

Additional beakers were established at all temperature-salinity combinations to determine the approximate ratio of *A. californiensis* to *A. clausi* resting eggs by rearing hatched nauplii to copepodites. These beakers contained the unsorted mixture of resting eggs of *Acartia* spp. and other accompanying species plus detritus which collected at the water-sucrose interface during centrifugation. The number of eggs in each beaker was variable, ranging between 50 and 250. Hatched nauplii were removed daily and transferred to new beakers at the next higher salinity (+5‰) and temperature (+2.5° C). Salinity and temperature were increased every 5th day to maxima of 15° C and 25‰. This was done to improve survival while avoiding abrupt change. Ratios were determined when most individuals had molted into the copepodite stages. Hatched nauplii from the Petri dishes were also reared when practical to the copepodite stages.

RESULTS

Field Population Cycle

The twice-weekly sampling program was adequate to follow the seasonal cycle and distribution of *A. californiensis* in upper Yaquina Bay. Only field data for 1972 are presented, since the population had similar cycles in 1973 and 1974.

The population range extended from Station 21 to Station 57 (Figure 1) during the months of maximum abundance (August, September). However, few adults or copepodites were ever present at these two boundary stations. The bulk of the population was restricted to the region from the vicinity of Station 29 to Station 45 with an approximate population center at Station 39. Location of the population center was not static at Station 39 because of the diurnal tides. It was occasionally found during sampling cruises downstream at Station 29 or upstream at Station 45.

The maximum density of *A. californiensis* observed on a given sampling day was considered to be the center of the population, regardless of location in the upper estuary. A plot of maximum density values for adults and copepodites I-V on successive sampling dates represents the seasonal cycle of the population (Figure 2). The persistent alternation between peak abundance of adults and copepodites is evidence that successive generations remain distinct. The fact that successive density estimates at the population center show such a refined feature creates confidence that the approach is valid.

Physical factors such as temperature and salinity can be correlated with population growth and decline on the premise that optimal conditions at a given time coincide with maximum spatial population abundance. Thus, given the population concentration from Station 29 to Station 45, mean temperature and salinity data (surface and bottom) at Stations 29 and 45 (Figure 3) can be considered to represent the lower and upper range of the most favorable physical conditions possible for growth of *A. californiensis* in the estuary at any given time. The means closely reflect the entire water column (4-6 m depth) as the upper estuary is well-mixed (Type D; Burt and McAlister 1959) during June to October with a maximum vertical gradient of 1°-2° C and 1-3‰. The fortnightly periodicity seen in the data is an effect of the progression of tidal stage upon twice-weekly sampling conducted during the fixed hours from 0900 to 1400. A sharp decline in salinity during late November and December (Figures 3, 4) occurred as a result of the beginning of the winter rains and resulting heavy runoff. Salinity in the upper estuary remained extremely low (Figure 4) until the following spring when rainfall and runoff decreased, and the salt wedge intruded up the bay.

The appearance in early June of *A. californiensis* copepodites occurred when water temperatures were between 15° and 18° C and salinities were 10-20‰ (Figure 3). Abundance gradually increased throughout June and much of July. A population explosion began in late July and continued throughout August, a period when water temperature and salinity were 17°-22° C and 20-31‰. The subsequent population crash in early

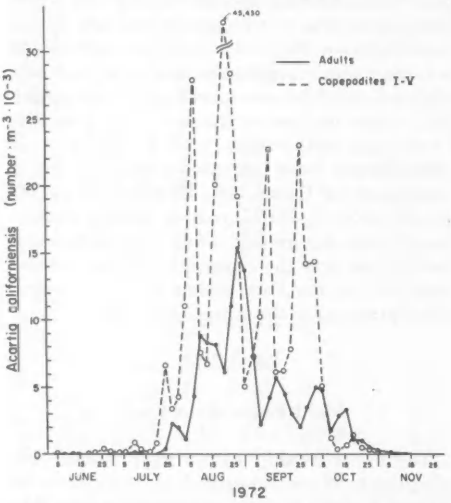

FIGURE 2.—Seasonal population cycle of *Acartia californiensis* in Yaquina Bay (1972) based on maximum abundance of adults and copepodites (I-V) observed on successive sampling days.

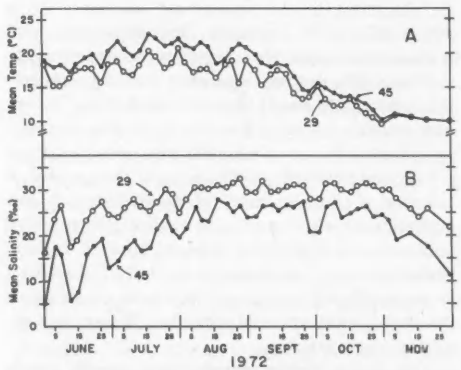

FIGURE 3.—Temperature (A) and salinity (B) profiles at Stations 29 and 45 during June to November 1972. Points represent means of surface and bottom values. Envelopes correspond to general range of most favorable physical conditions for *Acartia californiensis* population growth at a given time.

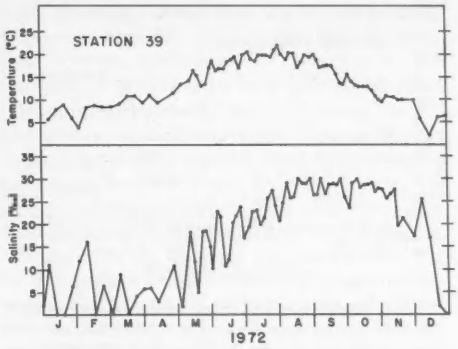

FIGURE 4.—Annual profile of bottom temperature (° C) and salinity (‰) at Station 39 in 1972. Values represent general range of temperature-salinity experienced by resting eggs in surface layer of sediments. December-May values from unpublished data of H. F. Frolander (School of Oceanography, Oregon State Univ., Corvallis, OR 97331).

September (19°-22° C, 25-30‰) was followed by a gradual decline to complete absence in late November. Production of nondormant eggs remained important throughout September, as evidenced by the large numbers of copepodites present in the water column. However, copepodite recruitment nearly ceased by the first week of October, indicating that most reproduction was likely in the form of resting eggs. Some nondormant eggs were still produced, however, since a small pulse of copepodites was seen in the last half of October. Mean temperature had dropped to 13°-15° C at the end of September when recruitment began to fail. The population was gone by December at a field temperature of 9°-10° C. Salinity remained high, relatively stable, and presumably in a favorable range (25-30‰) during the September-October decline and disappearance. Salinity began to drop only in November when *A. californiensis* was essentially absent from the water column.

Resting Egg Production

October Experiment (Preliminary)

Eggs collected on the third day of adult acclimation to 21°, 17°, 13°, or 9° C had essentially similar hatching rates and cumulative hatching success at a given temperature to eggs collected on the eighth day. The similarity in results indicates that *A. californiensis* can shift from production of nondormant eggs to production of resting eggs in only 1-2 days in response to a significant lowering of water temperature. The absence of significant changes in egg hatching time and viability with increasing adult acclimation time demonstrates that the eggs produced were not adversely affected by the rapid change in water temperature (2-4 h) at the beginning of the acclimation period. The only effect observed was an initially lower fecundity in those females which experienced the largest temperature changes (16.8° C to 21° C or 9° C). In these latter two cultures, fecundity increased with acclimation time.

October Experiment (Main)

Hatching successes of eggs spawned over the range of 9°-21° C give evidence that the type of egg spawned is a function of ambient temperature (Figures 5, 6). Experimental conditions and results are also summarized in Table 1. Females which spawned at 21° and 17° C (typical midsummer temperatures at Stations 29-45) produced nondormant summer eggs that developed normally at 21° and 17° C (Figure 5A, B). Development time was <36 h with nearly 100% of the eggs hatching. Lower hatching temperatures (13°, 9°, 5° C), however, were found to arrest development of summer eggs which then entered dormancy. The incidence of dormancy increased with decreasing hatching temperature: eggs spawned at 17° C had a total hatching success of 71% at 13° C compared with 35% at 9° C (Figure 5C, D) and 5% at 5° C (Figure 6). Thus dormancy in summer eggs is a response to low, unfavorable temperatures and may occur independently of parental influence.

More than adequate time (Table 2) was allowed in these experiments for "normal" hatching, given the prediction from a Bělehrádek function for *A. tonsa* (Zillioux and Gonzalez 1972) and the observed development rates for *A. clausi* (Landry 1975b). A subsequent increase in water temperature to 21° C broke the dormancy of the summer eggs previously incubated at 13° and 9° C (Figure 5C, D). Hatching resumed within a few hours at a rate similar to that observed earlier at 17° and 21° C (Figure 5A, B).

Mortality of summer eggs spawned at 17° C was low during the 11- and 15-day "holding" periods at 13° and 9° C (Figure 5C, D), evidenced by a final hatching success of 90-96% after increase to 21° C. However, dormant 21° C summer eggs experienced substantial mortality during the 15-day

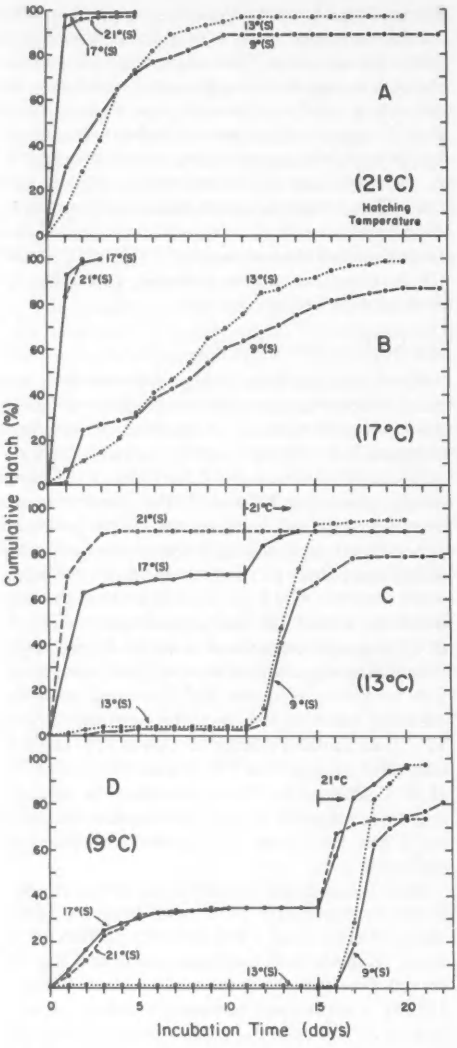

FIGURE 5.—Hatching success of *Acartia californiensis* eggs at: (A) 21° C, (B) 17° C, (C) 13° C, (D) 9° C in 25‰ salinity. Eggs spawned at different parental acclimation temperatures of 21°, 17°, 13°, and 9° C. Spawning temperatures are designated by (S). Hatching temperatures increased to 21° C on day 11 (C) and 15 (D).

holding period at 9° C (Figure 5D). Only 60% of the remaining eggs hatched following the temperature rise, resulting in a cumulative total of 74%.

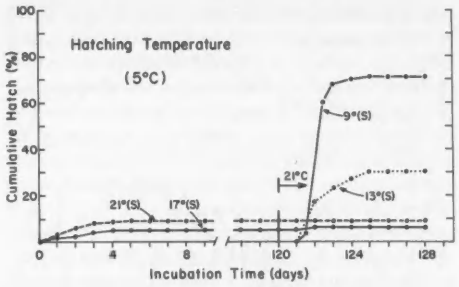

FIGURE 6.—Hatching success of *Acartia californiensis* eggs at 5° C in 25‰ salinity. Eggs spawned at 21°, 17°, 13°, and 9° C. Spawning temperature is designated by (S). Hatching temperature increased to 21° C on day 120.

Long-term survival of summer eggs was negligible at low temperature (120 days at 5° C). Only 1% of the 17° C spawned eggs subsequently hatched at 21° C. Many of the eggs remained normal in appearance, being greenish yellow, throughout the 120-day period. However, within 3-4 days at 21° C, nearly all dormant summer eggs had disintegrated. Most eggs probably died long before day 120, given the high mortality of 21° C spawned eggs after 15 days at 9° C (Figure 5D).

In comparison with dormant summer eggs, the eggs spawned at 13° and 9° C appear to be true resting eggs with an overwintering capacity. The final cumulative hatch of the two types of eggs was similar over the temperature range of 21°-9° C. However, there were major differences in hatching rates between eggs spawned at 9°-13° C and 17°-21° C at all five hatching temperatures tested (Figures 5, 6). For example, the 9°-13° C spawned eggs required 11 and 20 days at 21° and 17° C, respectively, to reach the final comparable hatch of 87-99%. This period was 10-20 times longer than that required by summer eggs.

While none of the 9°-13° C spawned eggs exhibited dormancy at 17° and 21° C, few hatched at the lower incubation temperatures. Only 3-4% hatched at 13° C in contrast to 70-90% for the summer eggs. Likewise only 0-1% at 9° C and 0% at 5° C hatched versus 35% and 5-10%, respectively, for the summer type (Figures 5D, 6).

Temperature was increased to 21° C on days 11, 15, and 120 for the 13°, 9°, and 5° C hatching treatments, respectively. Hatching resumed in all cases at a rate and with success similar to those of summer eggs. However, a 1-1.5 day delay occurred in each case before hatching resumed (Figures 5C,

D; 6). This delay, absent from the data on hatching of summer eggs following an identical temperature increase, is evidence of a difference in the character of dormancy in the two types of eggs.

Resting egg mortality was low during the 11- and 15-day incubation periods (Figures 5C, D). Approximately 96% and 80% final hatch occurred for eggs spawned at 13° and 9° C, respectively. The somewhat lower viability of the 9° C spawned eggs was also seen at hatching conditions of 17° and 21° C (Figure 5A, B). Survival remained high (71%) for 9° C spawned eggs following 120 days incubation at 5° C (Figure 6). In comparison, the 13° C spawned eggs had only 30% survival. This substantial difference in survival may not be important, as opposite results were found for the hatching success of resting eggs from the preliminary experiment under equivalent conditions (9° C spawn = 45%; 13° C spawn = 60% survival). The implication is that resting egg survival is about 50% after a 4-mo dormant period.

In most cases, hatching success at a given temperature was similar for eggs of a given type (summer or resting) spawned at different temperatures (Figures 5, 6). For example, 21° C spawned eggs displayed little difference in hatching time or success from 17° C spawned eggs at 21°, 17°, and 9° C. The discrepancy in summer egg hatching times and cumulative totals at 13° C was likely an experimental artifact since it was absent in the results of the preliminary experiment. Uye and Fleminger (1976) similarly reported finding no difference in hatching success at a given temperature for *A. clausi* eggs spawned at 17.5° and 13.5° C.

A notable exception to this pattern occurred for 13° and 9° C spawned eggs which were incubated at 21° and 17° C (Figure 5A, B). In both cases, the 9° C spawned eggs had a higher initial rate of hatching than 13° C spawned eggs. By day 5, this was reversed, and the rate for 13° C spawned eggs exceeded that for 9° C spawned eggs. It is possible that some of the 9° C spawned eggs had an enhanced metabolic rate relative to 13° C spawned eggs, caused by cold acclimation (suggested by Landry 1975b). Uye and Fleminger (1976) also found evidence that cold-acclimated eggs of *A. tonsa,* spawned at 6.5° C, tended to hatch more quickly at temperatures below 12.5° C than eggs spawned at 17.5° C.

Long-term exposure to low temperature resulted in abnormal development for some resting eggs. This was only seen in 5-12% of the 9° C spawned eggs incubated at 9° or 5° C for 120 days. Abnormalities of the newly hatched NI nauplii ranged from mild to strong structural deformation. Some nauplii possessed an enlarged labrum or fused appendages (e.g., second antennae and mandible); some lacked appendages of one side of the body. One nauplius had two severe constrictions which divided the body into three lobes. Many of the abnormal nauplii were alive, though weak, at the time of observation. Uye and Fleminger (1976) also reported finding deformed NI nauplii and postulated that osmotic stress from abnormal salinities may have caused the deformations. In this case, however, deformation must have resulted from long exposure to low temperatures, since salinity was maintained at a favorable concentration of 25‰.

November Experiment

Different hatching results were obtained using eggs spawned by females acclimated at the November field temperature of 12° C. Hatching patterns (Figure 7) indicate that both nondormant and resting eggs were produced concurrently in the population. This is in contrast to production of resting eggs only in the 13° and 9° C treatments of females collected in October for the main experiment (Figures 5, 6). The evidence for the presence of both egg types is the two different hatching rates which occurred at summer temperatures (Figure 7). The initial hatching at 21° and 17° C occurred within the first day, similar to summer eggs at identical temperatures (Figure 5A, B).

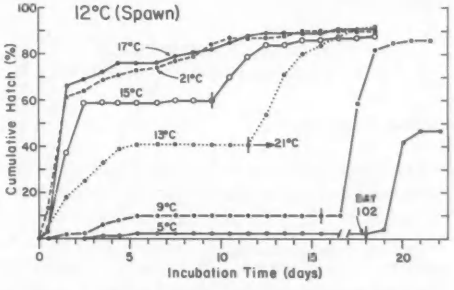

FIGURE 7.—Hatching success of *Acartia californiensis* eggs spawned by November-collected females at the field acclimation temperature of 12° C. Hatching temperatures varied from 21° C to 5° C; salinity was 25‰. Temperature increased to 21° C (denoted by vertical line) after variable periods of incubation below 17° C.

However, after reaching a total of 61-66% hatched, the rate decreased sharply with hatching continuing at a low, constant rate to a final total of 90-91% at day 16. The latter pattern resembles that found for resting eggs (13°, 9° C spawn) hatched at summer temperatures (Figure 5A, B). A comparable 56% hatch also occurred at 15° C within the first 2.5 days. However, development then ceased until temperature was increased to 21° C. Thus, at all three temperatures, approximately 60% of the eggs behaved as nondormant summer eggs, while the remaining 40% had characteristics of resting eggs.

Dormancy increased from 40% at 15° C to 98% at 5° C (Figure 7), presumably as a result of dormancy induced by low temperatures in otherwise nondormant eggs. This result is similar to that seen for summer eggs hatching at the lower temperatures (Figures 5C, D; 6).

Egg viability during short- and long-term dormancy was determined by increasing temperature to 21° C on days 9, 11, 15, and 102 for the 15°, 13°, 9°, and 5° C hatching treatments, respectively (Figure 7). Mortality was low during the 9-15 day incubation period at 15°, 13°, and 9° C with a final cumulative hatch of 85-91%. In contrast, only 45% of the dormant eggs incubated for 102 days at 5° C completed development into NI nauplii following temperature elevation. Probably few dormant summer-type eggs survived the long holding period at 5° C, given that about 40% of the eggs exhibited characteristics of resting eggs in 21°, 17°, and 15° C water. This conclusion is supported by the high mortality (99-100%) found for summer eggs incubated at 5° C for 120 days in the October experiment (Figure 6).

Hatching of Resting Eggs Collected in the Field

Salinity Experiment

The effect of salinity on hatching of resting eggs collected from field sediments was initially determined at 17° C, a temperature favorable for egg hatching (Figure 5) and population growth of *A. californiensis* (Figures 2, 3). Results presented in Figure 8 are the combined data for both *A. californiensis* and *A. clausi*, since their respective overwintering eggs could not be separated.

Hatching occurred at all salinities from 23.5‰ to 0‰ (Figure 8). Rates decreased only slightly with decreasing salinity from 23.5‰ (37%•day^{-1}) to 12.5‰ (31%•day^{-1}; day 2.5). Final hatch in this salinity range was 91-96%. Initial hatching rates below 12.5‰ decreased markedly, ranging from 26%•day^{-1} at 10‰ to 1.8%•day^{-1} at 0‰. These latter rates, while reduced, were nevertheless substantial over a 2-wk span. Overall hatching success by day 12 was 21%, 61%, and 88% of the resting eggs at 0‰, 5‰, and 8‰, respectively. Furthermore, hatching was continuing, even in freshwater, as indicated by the slopes of the curves, when the experiment was ended. In comparison, resting eggs of *Tortanus forcipatus* do not hatch in freshwater when temperature is favorable (Kasahara, Onbé, and Kamigaki 1975).

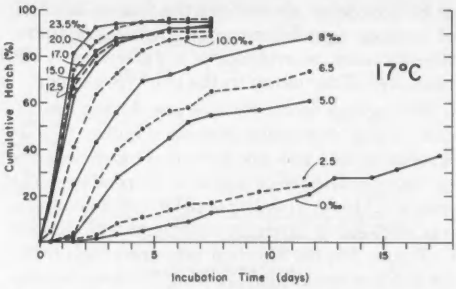

FIGURE 8.—Hatching success of field-collected resting eggs of *Acartia* spp. as a function of salinity (0-23.5‰) at 17° C.

The retarding effect of low salinity on hatching appeared to be limited to the actual process of naupliar escapement from the eggshell. Embryogenesis proceeded at similar rates (subjective observations) in all treatments (0-23.5‰), apparently independent of external salinity concentration. Developmental arrest, when present, normally occurred after the fully formed nauplius was visible inside the eggshell.

Exposure to low salinity (0-5‰) for varying periods during dormancy was not fatal for the majority of prehatch nauplii. In each case, high rates of successful hatching (Figure 9) quickly followed a salinity increase to 23.5‰. However, prehatch mortality of "holding" nauplii increased substantially as a function of salinity reduction when compared at equal time. This is seen in a final hatch of 79%, 71%, and 59%, following a salinity increase (day 12) to 23.5‰ for eggs previously incubated at 5‰, 2.5‰, and 0‰, respectively. Thus, an approximate 10% increase in mortality occurred for each 2.5‰ decrease in salinity below 5‰.

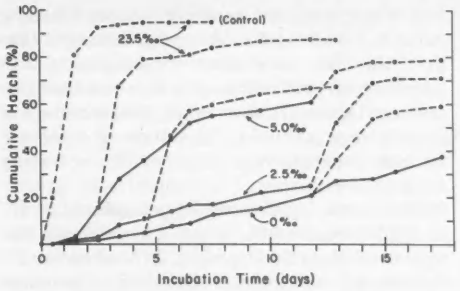

FIGURE 9.—Hatching success and viability ("holding" success) of *Acartia* spp. at 23.5‰ salinity (dashed line), following variable periods of exposure to low salinities (0-5‰) at 17° C. Initial hatching results at 23.5‰ used as a control.

Prehatch mortality also increased gradually with increasing time at low salinity (Figure 9). Total hatch in 23.5‰ after 2.5 and 12 days exposure to 5‰ was 87% and 79%, respectively. This corresponds to a loss of 8% viability within the first 2.5 days and 16% by day 12 as measured against the control hatch at 23.5‰. A comparable trend and loss rate occurred for 0‰ salinity-exposed eggs later hatching in 23.5‰. Losses in viability on days 4.5 and 12 were 27% and 36%, respectively.

The cause of death in prehatch nauplii is unknown, but presumably is related to exhaustion of energy reserves during the holding period. Mortality may also be partially caused by increased osmotic stress at progressively lower salinities. Eggs that died prior to hatching usually disintegrated with 2-3 days at 17° C.

The occurrence of naupliar mortality during the actual hatching process or within the following 24 h substantially increased at salinities below 12.5‰. This is shown by a comparison of cumulative hatching and subsequent naupliar mortality as a function of salinity on days 4.5 and 12 (Figure 10). Naupliar losses on day 4.5 increased from 1% at 12.5‰ to 73% at 5‰. Mortality was 100% at 2.5‰ and 0‰. Corresponding losses were 5-10% higher on day 12, indicating that survival following hatching decreased gradually with increasing time required to hatch.

Observation of hatching success in salinities below 8‰ revealed that many nauplii died during the hatching process or immediately thereafter. At 5‰, many of the dead nauplii were found only partially freed from the cracked-open eggshell. More typically, the nauplius was found lying next to the empty eggshell, indicating immediate death followed hatching. Some nauplii successfully hatched, but never unrolled. Others escaped the outer egg membrane, but died while still inside the osmotically swollen inner membrane. Eggs which had obviously cracked open prior to full development, and exhibiting an extrusion of cellular debris, were also occasionally seen at 0‰ and 2.5‰.

The specific effects of salinity on resting eggs of *A. californiensis* cannot be separated from those of *A. clausi* in the results above. However, supportive evidence indicates that eggs of both *Acartia* species hatched at substantial rates at all salinities from 0‰ to 23.5‰. For instance, 41% of the copepodites reared from viable nauplii during the course of the experiment were *A. californiensis*. While there is no information on possible differential mortality during culturing, an estimate of 41% is probably low for the percentage of *A. californiensis* resting eggs in the experiment. Initial rearing conditions actually favored *A. clausi*, a species that is much more euryhaline in Yaquina Bay. Thus, even when considering the lowest hatching rate at 0‰ salinity on day 17 (Figure 7), it is clear that the 37% hatch (100% mortality) had to include at least some *A. californiensis* eggs. Approximately another 40-50% of the holding eggs at 0‰ were no longer viable. Therefore, one can conclude that prolonged exposure of *A. californiensis* resting eggs to extremely low salinities at 17° C will result in death for the majority, whether it be from prehatch or posthatch salinity stresses.

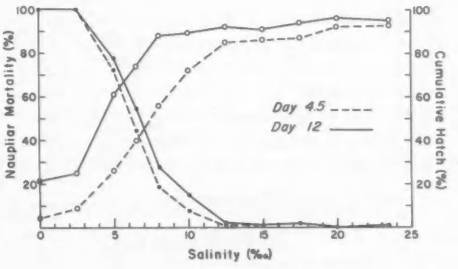

FIGURE 10.—Comparison of cumulative hatch of field-collected resting eggs of *Acartia* spp. (open circles) and subsequent mortality within first 24 h (solid circles) at salinities from 0‰ to 23.5‰. Results on day 4.5 (dashed line) and 12 (solid line) based on 3 replicates of 35 eggs at each salinity.

Salinity and Temperature Experiment

The effect of salinity on hatching of resting eggs was reexamined (Figure 11) at lower temperatures (15°, 12.5°, 10° C) which are marginal to unfavorable for growth of the *A. californiensis* population (Figures 2, 3). The basic intent was to determine, if possible, the lowest termperature-salinity combination(s) which could break diapause of the overwintering eggs.

General hatching patterns as a function of salinity (Figure 11) were similar to those observed at 17° C (Figure 8) in that hatching rates decreased with decreasing salinity at all three temperatures.

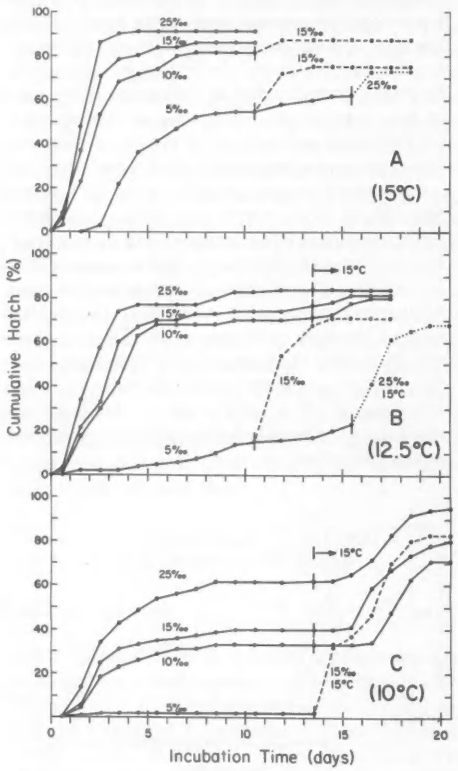

FIGURE 11.—Hatching rate and cumulative success of field-collected resting eggs of *Acartia* spp. in various salinities at: (A) 15° C, (B) 12.5° C, and (C) 10° C. Lower temperatures and salinities increased to 15° C and 15‰, respectively, after variable periods of incubation to determine short-term "holding" success at suboptimal conditions.

Lower temperatures similarly reduced hatching rates and final hatches at a given salinity. However, the interactive effect of temperature with salinity increased nonlinearly as temperature decreased (Figure 11). As a result, the percentage of resting eggs remaining in a state of dormancy became progressively larger with decreasing temperature.

Few *Acartia* spp. resting eggs incubated at 15° or 12.5° C (Figure 11A, B) failed to terminate diapause and begin development. As observed at 17° C, embryogenesis progressed to the final prehatch stage, apparently independent of external salinity. Subsequent holding time (pseudodormancy) depended on the interaction of salinity and temperature. For example, hatching rates at 25‰, 15‰, and 10‰, while progressively reduced, were still relatively high with very little dormancy evident. The majority of eggs hatched within 3-4 days. Final hatches were high and in a narrow range from 91-81% at 15° C to 84-71% at 12.5° C. However, some prehatch holding did occur at these higher salinities since an increase in salinity (10‰ to 15‰; Figure 11A) or temperature (12.5° to 15° C; Figure 11B) resulted in an additional 5-9% hatch.

Prehatch holding at 5‰ was increasingly more important with decreasing temperature (Figure 11A, B). At 15° C, the 5‰ hatching rate was greatly reduced, but was still substantial and similar to that seen at 17° C (Figure 8). Over 50% hatch was attained by day 7, with hatching continuing to 62% on day 15. Viability of the remaining eggs (38%) was low since a salinity increase to 25‰ only yielded an additional 11% hatch. In comparison, prehatch holding in 5‰ at 12.5° C (Figure 11B) was pronounced since the hatching rate was reduced to only 1-2% • day^{-1}. However, the holding dormancy was only a temporary condition since hatching continued throughout the 15-day exposure to 5‰. Viability was reduced but still substantial as seen in a final hatch of 68% in 25‰. Thus, hatching in 5‰ water at 12.5° C or 15° C would have probably continued until all eggs either hatched or died from exhaustion of energy reserves during the holding state.

Hatching results at 10° C (Figure 11C) were considerably different from results at 12.5° C and 15° C in that dormancy was a major factor at all salinities. For example, final hatches (prior to changes) at 25‰, 15‰, and 10‰ were 61%, 40%, and 33%, respectively. This represented a 23-38% increase in dormancy from that at 12.5° C. Persis-

tence of dormancy at 5‰ was nearly complete with only 2% hatch achieved.

The nature of continued dormancy at 10° C (Figure 11) was unusual in that both diapause and prehatch holding cooccurred. Dormant eggs remaining on day 13 at 25‰, 15‰, and 10‰ appeared to still be in diapause since no apparent change in coloration or internal structure occurred during incubation at 10° C. A subsequent 1-3 day delay in hatching after temperature was increased to 15° C is also indicative that the eggs were still in diapause (as seen in the October temperature experiments; Figure 5C, D). Copepodites reared from nauplii hatched at 15° C in the 25‰, 15‰, and 10‰ treatments after day 13 were found to be mainly *A. californiensis* (87%; $n = 23$). As a result, most of the eggs remaining in diapause at 10° C over the 25-10‰ range were probably those of *A. californiensis*.

In contrast to results at 25-10‰ (Figure 11C), diapause did not persist in eggs of either *A. californiensis* or *A. clausi* exposed to 5‰ at 10° C. The reason for this difference is not known. While only 2% of the eggs had hatched, nearly all remaining eggs had broken diapause and were in the final prehatch holding state many days before the temperature increase on day 13. The difference in the nature of dormancy is reflected by the rapid hatching rate with no delay period following the temperature increase. In spite of high viability seen after day 13, the termination of diapause and the failure to hatch at 5‰ and 10° C demonstrate that egg survival of both *Acartia* species was short-term and limited by available energy reserves.

Posthatch naupliar mortality within the first 24 h as a function of salinity at 15°, 12.5°, and 10° C was very similar to that shown for 17° C (Figure 10). The mortality range in 15‰, 10‰, and 5‰ water, for example, was 2-7%, 12-22%, and 80-100%, respectively, as compared with 2%, 15%, and 78% at 17° C. Typically, the percent survival decreased slightly at a given salinity as temperature decreased. Therefore, at salinities >10‰, survival was high with mortality primarily increasing with decreasing temperature. Below 10‰, the NI nauplii experienced increasingly heavy mortality primarily as a function of decreasing salinity.

Additional information on hatching behavior and fraction of *A. californiensis* resting eggs were obtained by a comparison of the proportions of copepodites reared from nauplii which initially hatched from unsorted egg mixtures at each temperature-salinity combination (Table 3). Hatching at the most optimal of the given experimental conditions for both species (15° C, 25-15‰) resulted in copepodite proportions of 51% and 62% *A. californiensis*. A similar percentage (54%) was observed at 12.5° C and 25‰. As these estimates are based on independent rearing treatments, it is reasonable to conclude that roughly 55% of the field resting eggs were those of *A. californiensis*. This result corresponds very well with other estimates of percent abundance determined in earlier unpublished experiments.

Copepodites of *A. californiensis* were absent in the cultures which initially hatched in 10‰ and 5‰ at both 15° and 12.5° C (Table 3). As nearly all resting eggs were previously found to terminate diapause at these lower salinities (Figure 11A, B), the absence of *A. californiensis* is the result of mortality during either prehatch holding or subsequent naupliar stages. This is verified, in part, by the increasing mortality of NI nauplii (*Acartia* spp.) below 12.5‰ (Figure 10). Furthermore, hatching rate differences over the range of 25-10‰ were small as shown in Figure 11A, B. For example, at 15° C, a total hatch of 86% and 81% was observed at 15‰ and 10‰, respectively. Yet, the proportion of *A. californiensis* copepodites was 62% at 15‰ and 0% at 10‰ (Table 3). Similarly at 12.5° C, only 6% survived to copepodites when hatched at 15‰ as compared with 54% at 25‰. It must be reemphasized that the temperature and salinity values referred to here and in Table 3 are hatching conditions only. Rearing was under more favorable conditions (see Methods). Therefore, as

TABLE 3.—Proportion of *Acartia californiensis* and *A. clausi* copepodites that survived following hatching at 12 temperature-salinity combinations. Temperature and salinity levels for rearing to copepodite stages were gradually increased to 15° C and 25‰ to increase posthatch survival (see text for further details).

Salinity (‰)	10° C			12.5° C			15° C		
	n	*A. clausi* (%)	*A. calif.* (%)	*n*	*A. clausi* (%)	*A. calif.* (%)	*n*	*A. clausi* (%)	*A. calif.* (%)
5	0	0	0	4	100	0	0	0	0
10	16	100	0	24	100	0	119	100	0
15	15	100	0	71	94	6	40	38	62
25	235	100	0	28	46	54	183	49	51

diapause was ended at all salinities at 12.5°-15° C, it is evident that individuals hatching from resting eggs of *A. californiensis* exposed to salinities below 15‰ experienced early death, even when temperature and salinity were increased to more favorable levels following hatching. As a result, these data can be used to define minimal hatching conditions for growth to maturity and can be correlated with the fall disappearance and summer repopulation of *A. californiensis* in Yaquina Bay.

Acartia californiensis copepodites were absent at all salinities at 10° C (Table 3). Absence over the range of 25-10‰ was probably the result of continued diapause of the resting eggs of *A. californiensis*, as previously demonstrated (Figure 11C). Some of the latter eggs may have hatched at 25‰, given the likelihood of a 62% hatch (Figure 11C) and an estimated resting egg ratio of 55% (Table 3). However, egg hatching at 15‰ and 10‰ (40-33%; Figure 11C) can be completely attributed to *A. clausi* since it composed ca. 45% of the resting eggs.

An unrelated but important observation concerns the hatching of a few *Epilabidocera longipedata* Sato (= *E. amphitrites* McMurrick) 10° C, 25‰) and *Eurytemora affinis* (Poppe) (10°-15° C, 5-25‰) from the unsorted resting egg mixtures used to obtain *Acartia* spp. ratios. Identification was made at the late copepodite stages. Neither species has previously been reported as possessing a resting egg stage. Both species are absent at Station 39 in Yaquina Bay during the winter months, insuring that the eggs were in diapause when collected.

DISCUSSION

Environmental Conditions Resulting in Egg Dormancy

Many shallow-water neritic and estuarine calanoid species with multivoltine life cycles are now known to survive long periods of adverse environmental conditions by facultative production of resting eggs. Field observations and laboratory results have demonstrated that this is true for *A. californiensis* in Yaquina Bay. After 4 or 5 successive generations with substantial recruitment (July-September 1972; Figure 2), the planktonic population declined rapidly and was gone by mid-November. The failure of recruitment in early October coincided with a decline in temperature below 15° C. Salinity remained relatively high and stable at 25-30‰, during the population disappearance, implying temperature dependence for the production of resting eggs (Figures 3, 4).

Experimental results confirmed the hypothesis that diapause in *A. californiensis* eggs is essentially a response of the spawning females to low temperatures, similar to that shown for *A. tonsa* (Zillioux and Gonzalez 1972), *Tortanus forcipatus* (Kasahara, Onbé, and Kamigaki 1975) and possibly *Pontella meadi* (Grice and Gibson 1977). The shift from summer egg to resting egg production occurred between 15° and 13° C (Figure 5), a temperature range comparable to that observed in the field. Salinity was not a factor, since it was maintained at a constant and favorable level (25‰) in all treatments. Food quantity and quality were excluded as factors by daily providing the adults with an ample ration consisting of three prey species. Photoperiod is known to influence induction of diapause in some cladocerans (cf.: *Daphnia magna*, Bunner and Halcrow 1977; *D. pulex*, Stross and Hill 1965). However, it was eliminated as a possible extrinsic factor by the use of continuous lighting.

The production of overwintering eggs was most likely initiated by changes, possibly hormonal, within the female in response to the extrinsic stimulus of adverse temperature. Extensive research on the physiology of insects has confirmed the regulation of diapause by hormones (e.g., Lees 1955; Sláma et al. 1974). Moreover, Carlisle and Pittman (1961) found differences in forebrain neurosecretions between summer and overwintering "dormant" CV copepodites of *Calanus finmarchicus* that resembled diapause in insects. Watson and Smallman (1971) similarly reported significant changes in small tissue patches in the head region of the cyclopoid copepod, *Diacylops navus*, that correlated with induction and cessation of diapause. Since dormant egg production can be rapidly induced in *A. californiensis* by lowering water temperature, it is probable that the controlling physiology is somewhat different.

The temperature-dependent maternal role in the induction of dormancy in *A. californiensis* eggs is contrary to results reported by Uye and Fleminger (1976) for *A. californiensis* (= *Acartia* sp. I) in a southern California lagoon. They concluded that egg dormancy in *A. californiensis* must occur independently of maternal influence since 90-100% of the eggs hatched at all temperatures in the annual field range (10°-25° C). Expo-

sure to salinity extremes was suggested as a possible cause of induced dormancy. Their conclusion, however, was based upon the hatching behavior of *A. californiensis* eggs which were spawned at 17.5° C. On the basis of my observations (Figure 5), these latter eggs were most likely all summer eggs which exhibited increasing dormancy below 10° C. It is likely that female-induced dormancy would have been observed if a spawning temperature below 15° C had been used.

Summer eggs of *A. californiensis* possess the capacity for short-term facultative dormancy when exposed to temperature below 15° C (Figure 5). Hatching resumed within hours following temperature elevation above 15° C. This type of arrested development, temporarily induced by unfavorable external conditions and ended with the return of a favorable environment, represents a state of "quiescence" as the term is used by Andrewartha (1952), Lees (1955), and Wigglesworth (1972) for other arthropod groups.

Quiescence of nondormant eggs at low temperatures is probably a characteristic of most calanoid species which inhabit highly variable environments such as estuaries and lagoons (Uye and Kasahara 1978). For example, Uye and Fleminger (1976) found that *A. tonsa* eggs which were spawned at 17.5° C (a favorable temperature) exhibited dormancy only at 7.5° and 5° C, a result which they also demonstrated for *A. californiensis*. In both species, survival during dormancy at 7.5° and 5° C was of short duration, since no hatching occurred following a temperature elevation after 28-30 days. The lack of long-term viability is supporting evidence that the respective eggs were in a quiescent state and not true resting eggs.

In each species, the percentage of quiescent summer eggs increased as temperature decreased. However, quiescence occurred at significantly higher temperatures in eggs of *A. californiensis* from Yaquina Bay, shown by a 35% hatch at 10° C (Figure 5D), as compared with 100% for the southern California population (Uye and Fleminger 1976). Both sets of eggs were spawned at 17° or 17.5° C. The considerable difference in thermal induction of quiescence in summer eggs may represent a genetic gradient reflecting the latitudinal separation of the two populations. Selection for quiescence in this warmwater species is probably more important in Oregon estuaries because of lower water temperatures (2°-22° C range) and longer winters (Figure 4). Less of a selective advantage would exist in California estuarine and lagoonal waters with a narrower annual range of 10°-25° C (from Uye and Fleminger 1976). Furthermore, any genetic gradient caused by differential selective pressures would be reinforced by the localized confinement of populations within estuaries or lagoons, which must greatly reduce gene flow.

The adaptive value of quiescence may be greatest in temperate estuaries (e.g., Yaquina Bay) where eggs in the bottom sediments typically experience large variations in temperature over successive tidal cycles. However, since viability of *A. californiensis* eggs in the quiescent state at low temperatures is limited to 1-2 mo, as shown above (Figures 5, 6) and in figure 5F of Uye and Fleminger (1976), the importance of quiescence in overwintering must be considered negligible.

Summer and resting eggs of *A. californiensis* may cooccur in equal proportions in the cumulative spawn at temperatures below 15° C as shown in the November experiment with females which spawned at their field acclimation temperature of 12° C (Figure 7). Zillioux and Gonzalez (1972) reported similar spawning results for *A. tonsa* females at acclimation temperatures of 9°, 11.4°, and 14.5° C. In each case, approximately 50-60% of the eggs were nondormant and hatched. It is not known from these data if the same female can produce both egg types at once. It is likewise not known if a female producing only resting eggs at lower temperatures can switch back to summer egg production if temperature increased above 15° C. These questions will need to be resolved by observations on individual females.

There is an apparent discrepancy between the November and October observations. Females collected from 15° C water in October produced exclusively dormant eggs when rapidly cooled to 13° or 9° C. It is reasonable to have expected all of the November eggs spawned at the field acclimation temperature of 12° C to have also been dormant, given the October results. Perhaps there are effects upon the initiation of dormant egg production from both low temperature to which a female is fully acclimated and from sudden temperature reductions. Response to the latter stimulus would protect against more than usually moderate cooling rates in the fall. Given normal field conditions, however, there probably is considerable variation between individual females in the population in the threshold temperature which induces dormant egg production. As a result, cooccurrence of both egg types would be expected during a significant

portion of the fall population decline. Some field evidence of this is seen in the weak pulse of copepodites found in late October, indicating that substantial hatching did occur below 15° C earlier in the month (Figures 2, 3).

Termination of Diapause and Population Reappearance

Hatching of field-collected resting eggs of *Acartia* spp. at various temperature-salinity combinations indicates that termination of dormancy is essentially temperature dependent. However, hatching rates and survival are regulated by salinity. My conclusions with respect to *A. californiensis*, based on the often disparate observations, are:

1. Approximately half of the experimental resting eggs were *A. californiensis*.
2. Embryogenesis and hatching occurred at all salinities tested at 12.5°-15° C (5-25‰) and 17° C (0-23.5‰).
3. Diapause persisted at 10° C over the range of 10-25‰, while embryogenesis occurred at 5‰.
4. Hatching was retarded at low salinities, particularly below 10‰.
5. Developmental arrest in low salinity normally occurred at the last stage of embryogenesis. Viability of "holding" prehatch nauplii was limited to 1-2 mo, depending on temperature.
6. Mortality losses were increasingly severe below 10‰ for hatched nauplii and substantial for "holding" eggs.
7. No nauplii survived to reach the copepodite stages at salinities below 15‰ at 12.5° C or at any salinity at 10° C.

Exposure to low temperatures over a prolonged period (comparable to cold stratification for seeds of many temperate, deciduous plants) is unnecessary for the release of diapause in *A. californiensis* overwintering eggs. This is probably the normal condition for most *Acartia* species (see Zillioux and Gonzales 1972 and Uye and Fleminger 1976). It is not universal, however, as the resting eggs of *Pontella meadi*, a neritic species, require a chilling period before hatching can occur (Grice and Gibson 1977). A similar requirement is implied but not conclusively demonstrated for resting eggs of *P. mediterranea* and *Centropages ponticus* (Sazhina 1968). Overwintering eggs of some freshwater calanoids (e.g., *Diaptomus oregonensis*, Cooley 1971) are also known to require exposure to low temperatures prior to hatching.

While chilling is unessential for termination of diapause in *A. californiensis* resting eggs, some effects from chilling were observed. For example, all field-collected eggs were found to commence development at 12.5° C (Figure 11) while laboratory-spawned eggs terminated diapause only above 15° C (Figures 5, 6, 7). Thus, exposure to winter temperatures appears to lower the hatching threshold. The time required is unknown but may be quite short. Newly spawned resting eggs initially hatched at very low rates when incubated at 17° or 21° C (Figure 5). However, after 11 and 14 days of chilling, hatching rates approached those of summer eggs when placed in favorable temperatures.

The "holding" phenomenon induced by low salinities represents a second type of short-term quiescence in *A. californiensis* resting eggs. It differs from the temperature-induced quiescent state seen in summer eggs in that quiescence does not set in until the final stage of embryogenesis. In addition, salinity-induced quiescence is much weaker, since hatching continues at low levels. In these aspects, it closely resembles the dark inhibition of summer egg hatching of *A. clausi* (Landry 1975a). Development of *A. clausi* eggs in the dark proceeds to the prehatch naupliar stage before "holding" occurs. Viability of eggs in this darkness-induced quiescence is even shorter than that of *A. californiensis* in low salinity-induced quiescence. Uye and Fleminger (1976) and my own data (unpubl.) indicate it is 20-25 days.

On the basis of field collections in February, experimental results and the temperature and salinity cycles in the field, significant hatching (or embryogenesis followed by holding) of resting eggs must occur over much of the year. Low oxygen tension in sediments, while important in inhibiting hatching (Kasahara, Onbé, and Kamigaki 1975), is probably not a critical factor, since resting eggs in the bottom sediments are continually exposed to oxygenated surface layers by turbulence and erosion. Termination of diapause does not always coincide with the presence of favorable environmental conditions for naupliar growth. Those resting eggs which undergo development and then either enter quiescence or hatch during the winter-spring months, a period of very low salinities, must be soon lost. Such a process would partially account for the seasonal decline in resting egg numbers in the sediments with

increasing time as observed by Kasahara, Uye, and Onbé (1975). Successful repopulation is possible at any point in spring that daily mean salinity is in excess of 10‰, which usually occurs in early June. Production of resting eggs in the annual cycle of *A. californiensis* is thus viewed as a "leaky" population diapause that is consistent with the opportunistic nature of estuarine copepod species.

It is possible that the leaky character of the diapause is retained because of the occasional success of the early-hatching portion of the population in years with early termination of winter rains. In those years, this fraction of the population would be strongly favored by the end of the growing season because of its early start. In years with prolonged spring rains, the late-hatching fraction would be favored. Variations in the weather cycle, thus, may prevent development of absolute and restrictive requirements for termination of diapause.

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AERIAL CENSUS OF THE BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, IN A REGION OF THE TEXAS COAST

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ABSTRACT

On five replicate aerial surveys in late March 1978, the bottlenose dolphin, *Tursiops truncatus*, herds were sighted and their numbers estimated in 21 strip transects flown across bays and channels between barrier islands and the coast from Port Aransas northeast to Matagorda, Texas. The transects were spaced at 4.63 km intervals and herds were scouted in about 800 m wide strips totaling 436 km in length, providing approximately 17% coverage of the area. On surveys 1-4 (survey 5 was excluded from population calculations because it was conducted in adverse weather) 133 bottlenose dolphin herds were sighted, containing an estimated 916 animals. Within these strips the mean heard size was 6.95 animals and mean herd density was 0.0947/km², extrapolating to a population estimate of 1,319 dolphins and a density estimate of 0.752/km² for the entire area. These figures are relatively high in contrast to recent studies in other environments. About half the herds were feeding and approximately one-third were traveling. Sightings were most frequent in ship channels, shallow areas inside barrier islands, and near shore. There were several sources of bias in our measurements, and we consider the results to be conservative.

In the waters under jurisdiction of the United States, live capture of marine mammals is now limited by law to those species that are used for public exhibition and scientific research. With the exception of certain pinnipeds, the greatest demand is for the bottlenose dolphin, *Tursiops truncatus* Montagu, the most tractable of the smaller cetaceans.

This recent management regime has generated a need for assessment of marine mammal stocks that consider population size and reproductive rates of potentially impacted species (Odell et al.[6]). Obviously, rigorous density estimates are an essential starting point for such studies, but despite the long history of a live fishery for bottlenose dolphins (Townsend 1914) there are scant population data on which to base management decisions (Odell 1975).

The majority of bottlenose dolphins that are readily available for capture dwell in the coastal and inland waterways of Florida and the other states bordering the Gulf of Mexico. In such environments several factors make *T. truncatus*, in contrast to pelagic odontocetes, ideally suited for synoptic studies from aircraft: many of the environments are semienclosed waters of limited dimensions, the herds are usually small thus individuals can be relatively accurately counted, and *T. truncatus* is generally the only small cetacean in the area and therefore easily identified. Accordingly, recent studies of bottlenose dolphins off the northern Gulf of Mexico and the Indian River area of Florida have used and refined aerial survey tactics and methods (Leatherwood et al. 1978; Leatherwood 1979; Leatherwood and Platter[7]; Odell and Reynolds[8]). Using similar procedures

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[6]Odell, D. K., D. B. Siniff, and G. H. Waring (editors). 1975. *Tursiops truncatus* assessment workshop. Final Report, U.S. Marine Mammal Commission, Contract MM5AC021, 141 p. Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149.

[7]Leatherwood, S., and M. F. Platter. 1975. Aerial assessment of bottlenosed dolphins off Alabama, Mississippi and Louisiana. *In* D. K. Odell, D. B. Siniff, and G. H. Waring (editors), *Tursiops truncatus* assessment workshop, p. 49-86. Final Report, U.S. Marine Mammal Commission, Contract MM5AC021. Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149.

[8]Odell, D. K., and J. E. Reynolds III. 1978. Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, on the west coast of Florida. Draft - Final Report, Marine Mammal Commission, Contract MM5AC026, 55 p. Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149.

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we report here on the size and density of the bottlenose dolphin population in the Port Aransas Pass-Matagorda Peninsula region of the Texas coast as observed in late March 1978 and compare the density figures with those obtained in the previous studies. Observations on *T. truncatus* distribution, behavior, sighting cues, and the perpendicular distances of the sightings, and alternative procedures and results are also presented and discussed.

STUDY AREA AND METHODS

Based on previous research (Leatherwood et al. 1978), a strip transect was designed (Eberhardt 1978). The dolphin herds were sighted and their numbers estimated within strips theoretically 804.5 m wide (0.435 n.mi.). All sightings, regardless of the numbers of animals, were statistically considered as a herd, and the term is used here in the general sense of a grouping of animals without implying more complex behavior. To achieve precision the same area was surveyed during five replicate flights. The extent of the area surveyed was limited to dimensions that could be covered in 7-8 h of flying time and that would provide approximately 17% coverage of the area on any one replicate survey.

The surveyed territory extended along 160 km (86 n.mi.) of the central Texas coast from Port Aransas at the northern end of Corpus Christi Bay to the base of the Matagorda Peninsula (Figures 1-3). This terrain is a complex of bays, bayous, lakes, and channels bordered seaward by long, low barrier islands. Convoluted arms of the larger bays extend inland into river deltas surrounded by agricultural lands. Marshes fringe much of the barrier and outer bay shorelines and numerous sand and shell reefs, small islands, and spoil dumps interrupt the water areas. Extensive shoals are covered by water of <1 m, and the deeper parts of the bays are limited to about 4 m depths. Oil well platforms and well heads are numerous in some parts of the bays and man-made

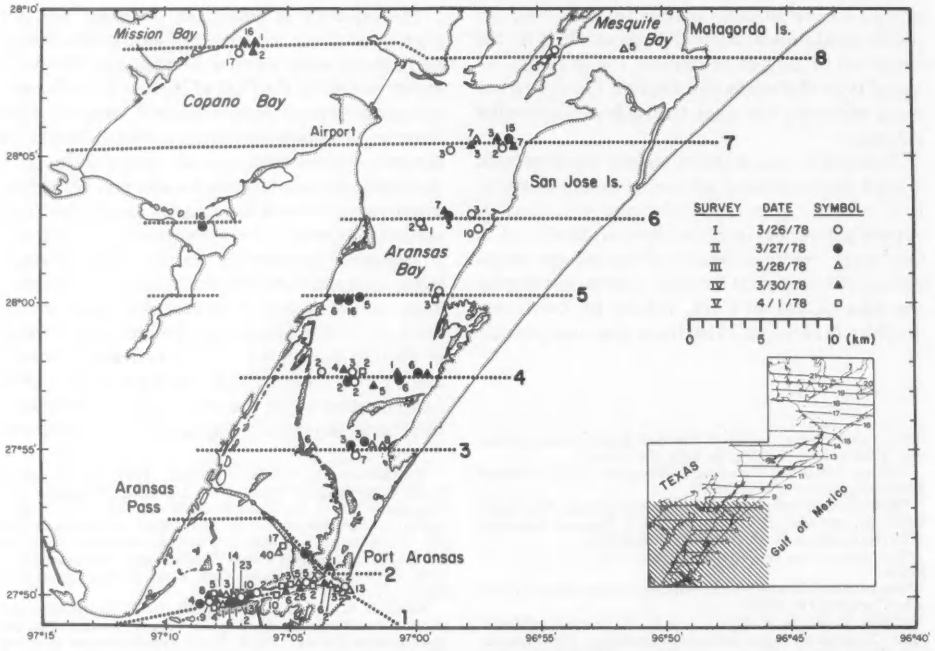

FIGURE 1.—Distribution of bottlenose dolphin herds and their estimated numbers from Aransas Pass to Mesquite Bay (transects 1-8), Texas.

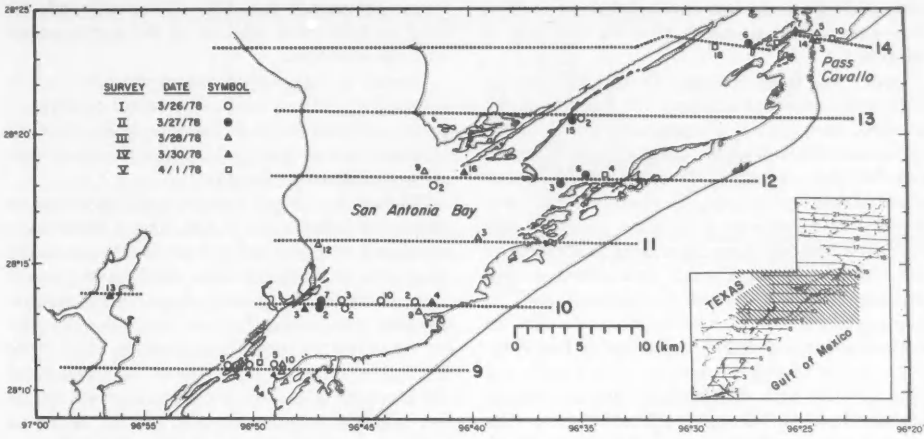

FIGURE 2.—Distribution of bottlenose dolphin herds and their estimated numbers from Ayres Bay to Pass Cavallo (transects 9-14), Texas.

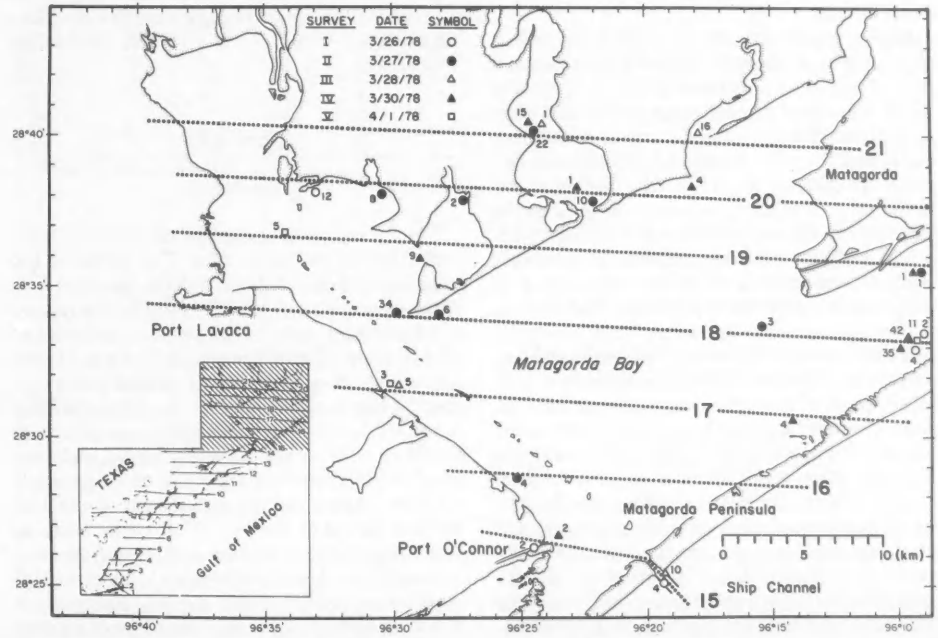

FIGURE 3.—Distribution of bottlenose dolphin herds and their estimated numbers from Port O'Connor ship channel to Tres Palacios Bay (transects 15-21), Texas.

cuts and channels run through the area. Five channels, two man-made, open to the Gulf of Mexico.

Operating from Aransas County Airport, a high-wing, four-seat airplane was flown along 21 transect lines spaced at approximately 4.63 km (2.5 n.mi.) intervels across the study area (Figures 1-3). With some exceptions the transect lines were oriented due east to west. To provide a reference point with a previous population study (Shane 1977) the first two lines were bent to conform to the narrow Corpus Christi and Aransas ship channels (Figure 1). Line 8 was jogged slightly to the north over the Lamar Peninsula so that its western extension would cross Mission Bay (Figure 1). Lines 14 and 15 were altered to overfly the Pass Cavallo and ship channel entrances into Matagorda Bay in the region of Port O'Connor, the location of a proposed *T. truncatus* study. In 12 cases the transects were interrupted by land that divided them into two or more parts, so that in all, 42 overwater crossings were flown. Eight of these crossings were 2 km or less in length while the longest was 42 km. Their average length was 10.2 km. Time of these crossings ranged from <1 to about 18 min.

Most transects were flown at 167 km/h and an altitude of approximately 152 m (500 ft). The first part of transect 1 was flown at 213 m (700 ft) to safely maneuver around large cranes and other structures. When not fully occupied with flying the plane, the pilot searched for bottlenose dolphins. An observer sat in the right front seat next to the pilot. This observer also functioned as the "navigator," talking the pilot onto transect landmarks, calling out the start and stop times for each transect, and charting the dolphin sightings. Two observers sat in the rear of the plane. The observer in the right seat mainly functioned as a recorder who kept a transect log noting the time of starting and ending of each transect and comments on visibility, weather, and other observations of interest. A sighting form was also kept in which was noted: the observer making the sighting, the nature of the observation which first alerted us to the presence of a dolphin herd, the sighting cue; the estimated numbers of adult animals and calves and their assumed behavior; and the estimated right angle, or perpendicular, distance of the sighted dolphin herds from the plane's track. While a strip transect design had been planned, the perpendicular distance estimations were essential for alternative dolphin density calculations utilizing line transect theory (Seber 1973). If time allowed, the herd configuration relative to the environment was also sketched.

Because of the low flying speed, the airplane was relatively quiet and voice communication between party members was feasible. The shortness of the transects and rest intervals between transect lines alleviated observer fatigue.

Observers searched outward to about 400 m (we estimated distances in yards). This distance was estimated with the aid of tape markings on the wing struts that had been calibrated against range marks on the landing strip. When a dolphin sighting was made, the pilot deviated from the transect line and usually orbited the herd twice while all observers counted the animals and noted the presence of calves. A consensus opinion was scored for these counts. Rarely only one circle was necessary, and on occasion three or more circuits were flown before the observers felt confident with the count. On occasion, individual animals or small herds could not be relocated and limited data based on the original sighting were logged.

Two observers worked all the flights, whereas one person was relieved as recorder-observer for the last three flights. The same pilot flew the plane on surveys 1-4. A different pilot took over on the last survey.

RESULTS

Operations

The survey design called for six replicate transect runs on successive days. The period of the operation (26 March-1 April 1978), however, was plagued by strong winds (33-46 km/h) that caused a 1-day postponement of survey 4, cancellation of survey 6, and affected the results of survey 5 to the extent that those data are of limited value (the specific effects of weather on the survey will be discussed later). Weather conditions were good to excellent on two runs, surveys 2 and 4, and marginal to fair on surveys 1 and 3. A malfunctioning airplane engine caused curtailment of the last three transects on survey 2. These were made up at the end of survey 4 under similar environmental conditions. A total of 436 track kilometers (235 n.mi.) was flown on each survey. Assuming a 402.25 m scan on each side of the aircraft, an area of 351 km^2 (102 $n.mi.^2$) was searched. With the 4.63 km transect line spacing, this would repre-

sent about 17% coverage of the survey area on any one replicate.

Dolphin Counts

During the first four survey flights 133 dolphin herds were sighted, containing an estimated 916 animals. A mean of 33.3 herd sightings per survey, composing 229 dolphins, was calculated for the four flights (Table 1). On survey 5, affected by adverse weather, only 19 herds estimated to contain 107 dolphins were sighted. Because these scores fell well below two standard deviations of the mean that was calculated for the first four replicates (Table 1), the results of survey 5 were excluded from our population calculations. Data from the last survey were used, however, for analyzing behavioral observations, sighting cues, and the perpendicular distances of dolphin herds from the trackline.

TABLE 1.—Bottlenose dolphin herd sightings, individuals, and calves estimated on surveys 1-4 Port Aransas to Matagorda, Texas.

Date (1978)	Survey number	Total no. of herds	Total no. of animals	Total no. of calves	Percent of calves
Mar. 26	1	36	175	17	9.7
Mar. 27[1]	2	36	260	17	6.5
Mar. 28	3	29	209	20	9.6
Mar. 30	4	32	272	31	11.4
Total		133	916	85	
Mean		33.3	229.0	21.3	9.3
SD		3.4	45.2	6.7	2.0

[1]The last four transects were run on March 30.

Calves

Among the animals sighted in surveys 1-4, some 85 were classified as calves, and they represented 9.3% of the total population observed (Table 1). Because the surveys were made just prior to the peak of the calving season, it was not always possible to differentiate between older calves of the year and young yearlings. Some 13 animals were in this questionable category.

Herd Size and Herd Density

While the estimated sizes of herds ranged from 1 to 42 animals, generally the aggregations were small. Groups of two and three *T. truncatus* represented the mode and composed 28.6% of all sightings, and 96 of the 133 sightings (72.2%) were composed of 7 or less animals (Figure 4).

FIGURE 4.—Frequency distribution of bottlenose dolphin herd sizes on surveys 1-4, Port Aransas to Matagorda, Texas.

The mean herd size for each daily survey replicate was computed as:

$$\bar{h}_j = \sum_{i=1}^{n_j} \frac{h_{ij}}{n_j} \qquad (1)$$

where $\bar{h}_j$ = mean herd size,
h_{ij} = herd size of the ith sighted herd on replicate j,
n_j = the number of herds sighted during replicate j.

The estimated herd density for each replicate was obtained from:

$$\hat{D}_j = \frac{n_j}{a} \qquad (2)$$

where $\hat{D}_j$ = the estimated herd density on replicate j,
a = the surveyed area in km^2,
n_j = is defined as before.

These calculations produced a mean herd size of 6.95 and a mean herd density of 0.0947/km^2 (Table 2).

Estimated Population Size (Numbers of Dolphins)

In previous aerial assessments of bottlenose dolphin populations by Leatherwood and his coworkers, variance of the population size was calculated according to Goodman's (1960) equation for estimating the variance of a product of two independent variables. However, in these cases Goodman's equation was used to estimate variance of the mean population size over all the replicates

TABLE 2.—Basic terms and figures for population size and density estimates of bottlenose dolphin in the Texas bays resulting from replicate surveys 1-4.

Survey number (replicate)	Mean herd size ($\bar{h}_j$)	Variance mean herd size (Var $\bar{h}_j$)	Herd density (no./km²) ($\hat{D}_j$)	No. of dolphins ($\hat{N}_j$)	Variance no. of dolphins[1] (Var $\hat{N}_j$)	Dolphin density (no./km²) ($\hat{d}_j$)	Variance dolphin density[2] (Var $\hat{d}_j$)
1	4.86	0.613	0.1026	1,008	58,828	0.575	0.0175
2	7.22	0.918	0.1026	1,498	100,613	0.854	0.0326
3	7.21	1.967	0.0826	1,204	103,000	0.685	0.0334
4	8.50	2.994	0.0912	1,567	175,232	0.893	0.0569
Mean	6.95		0.0947	1,319		0.752	
SD	1.52		0.0097	260.4		0.148	
SE	0.76		0.0049	130.2		0.074	
SE from theory					[3]189.43		[4]0.1080

[1]From Equation (9).
[2]From Equation (12).
[3]From Equation (10).
[4]From Equation (13).

and not the variances of each replicate. Quinn[9] has suggested a more refined treatment that is applicable if two conditions are met: the numbers of sightings for each replicate follows a Poisson distribution, and no real differences exist in the replicate herd densities. If these assumptions hold, a variance can then be legitimately computed for each replicate survey and these numbers pooled to produce a more precise estimate of mean population size variance. Accordingly, we proceeded as follows. The estimation of the population size for each replicate was calculated as:

$$\hat{N}_j = A\hat{D}_j\bar{h}_j \tag{3}$$

where $\hat{N}_j$ = estimated population size on replicate j,
A = total area assumed to be 5.76× of the searched area (a),
$\hat{D}_j$ = estimated herd density on replicate j,
$\bar{h}_j$ = mean herd size on replicate j.

Results are shown as "number of dolphins" in Table 2.

The computed variance of the estimated population size for each replicate was:

$$\text{Var}\,\hat{N}_j = A^2\,\text{Var}(\hat{D}_j\bar{h}_j) \tag{4}$$

which simplifies to:

$$\text{Var}\,\hat{N}_j = \left(\frac{A}{a}\right)^2 \text{Var}\,(n_j\bar{h}_j) \tag{5}$$

where a is assumed to be 17% of the total area (A).

The estimated variance of mean herd size within replicates was then estimated from:

$$\hat{\text{Var}}\,\bar{h}_j = \sum_{i=1}^{n_j} \frac{(h_{ij}-\bar{h}_j)^2}{n_j\,(n_j-1)}. \tag{6}$$

Following Elliott (1971), a chi-square value utilizing the index of dispersion was computed for the number of herd sightings on replicate surveys 1-4 to test agreement with a Poisson series. The index of dispersion was 0.35 with a resulting χ^2 value of 1.05. These values support the Poisson distribution assumption. This allows us to consider the variance of replicate herd sightings as equal to the numbers of herd sightings. Thus:

$$\hat{\text{Var}}\,n_j = n_j. \tag{7}$$

Using the chi-square test again we also found that there was no difference at the 5% significance level in the herd densities of the replicate surveys. The mean herd size ($\bar{h}_j$) and the numbers of herds sighted (n_j), however, were obtained from the same set of observations, and as one reviewer has rightly pointed out, it is not known if in fact these estimates were independent. We therefore tested for interrelationship using Spearman's Rank Correlation Test (Zar 1974). Finding no demonstrable correlation at the 5% significance level, we proceeded to treat the results of the replicate surveys generated from Equation (5) in terms of Goodman's (1960) equation for estimating the variance of a product as suggested by Leatherwood et al. (1978). Thus:

$$\hat{\text{Var}}\,\hat{N}_j =$$

$$5^2(n_j^2\,\hat{\text{Var}}\,\bar{h}_j + \bar{h}_j^2\,\hat{\text{Var}}\,n_j - \hat{\text{Var}}\,n_j\,\hat{\text{Var}}\,\bar{h}_j), \tag{8}$$

and substitution of n_j for $\hat{\text{Var}}\,n_j$ results in:

[9]Terrance J. Quinn II, Center for Quantitative Science, University of Washington, Seattle, WA 98195, pers. commun. to S. Leatherwood, March 1978.

$$\hat{\text{Var}}\,\bar{N}_j = 5^2(n_j^2\,\hat{\text{Var}}\,\bar{h}_j + \bar{h}_j^2\,n_j - n_j\,\hat{\text{Var}}\,\bar{h}_j)\,. \quad (9)$$

Before proceeding, a one-way analysis of variance with unequal sample sizes was performed on herd sizes with a $\log_{10}$ transformation for counts. No significant differences ($\alpha = 0.05$) between replicate herd sizes were found, thereby allowing the pooling of the four variances as:

$$\hat{\text{Var}}\,\bar{N} = \hat{\text{Var}}\left(\frac{\sum_{j=1}^{4}\hat{N}_j}{4}\right) = \left(\frac{1}{4}\right)^2 \sum_{j=1}^{4}\hat{\text{Var}}\,(\hat{N}_j)\,. \quad (10)$$

These computations produced an estimated mean *T. truncatus* population size of 1,319 with a standard error (SE) of 189 (Table 2).

The susceptibility of the above analysis to possible nonindependence of the mean herd size and herd density parameters was recognized by Leatherwood et al. (1978), and they suggested that mean herd size be established in preliminary flights before the herd counting phase of the survey is initiated. In the case of our work, however, because of inclement weather and limited resources we decided to make as many replicate surveys as possible rather than dividing the flight functions.

Despite the assurance of ranking tests, if independence between h_j and n_j does not hold, use of Equation (9) will probably underestimate the variance of N_j. An alternative more robust approach suggested by one reviewer was to compute the SE of the replicate estimates of numbers of dolphin on the four surveys (Table 2). This procedure produces a SE of 130.0 which is reasonably close to the theoretical value of 189 obtained from Equation (9) and tempers to some extent doubts of the validity of this approach.

Estimated Dolphin Density

For comparative purposes we also estimated the density of dolphins in the study area from:

$$\hat{d}_j = \hat{D}_j\bar{h}_j = \frac{n_j}{a}\bar{h}_j\,. \quad (11)$$

The same rationale and procedures for calculating the replicate and overall variances of population estimates were used to calculate the variances for dolphin density. Thus:

$$\hat{\text{Var}}\,\hat{d}_j = \frac{1}{a^2}(n_j^2\,\hat{\text{Var}}\,\bar{h}_j + \bar{h}_j^2\,n_j - n_j\,\hat{\text{Var}}\,\bar{h}_j) \quad (12)$$

and

$$\hat{\text{Var}}\,\hat{d} = \left(\frac{1}{4}\right)^2 \sum_{j=1}^{4}\hat{\text{Var}}\,\hat{d}_j\,. \quad (13)$$

This treatment gave an estimate of 0.752 dolphins/km^2 with an SE of 0.074. The SE calculated from the variance of the mean of the replicates was 0.108 (Table 2).

Comparisons with Other Population Studies

We can roughly compare our counts from the Aransas Pass area with those of Shane's (1977) who counted *T. truncatus* in the same area from a skiff run on a meandering course through the ship channels and cuts almost on a daily basis over a 1-yr period. For March and April 1977, her mean was 95 dolphins. The mean of our scores for transects 1 and 2 that covered part of her study area was 53. Considering the differences in methods and area covered, the results do not seem unreasonably diverse.

Our mean density estimate for all transects is compared with the results of recent aerial surveys of *T. truncatus* populations in waters adjacent to Florida, Mississippi, and Louisiana in Table 3. While it is clearly tenuous to contrast densities from different environments, it is worth noting that the two semienclosed areas, Indian River, Fla., and the Texas bays, appear to support similar densities, 0.52 dolphins/km^2 and 0.75 dolphins/km^2, respectively. The mean percent of the calves

TABLE 3.—Density estimates of bottlenose dolphin populations in southeastern U.S. coastal waters, based on recent aerial surveys. There are considerable differences in the nature and extent of the areas covered in these studies, thus the results are not strictly comparable.

Location	Reference	Dolphins per km^2	Dolphins per n.mi.^{2}
Florida			
Indian River	Leatherwood 1979	0.52	1.79
Florida[1]	Odell and Reynolds		
West coast	(text footnote 8)	0.27	0.93
Mississippi	Leatherwood et al.		
Gulf coast	(1978)	0.23	0.79
Louisiana	Leatherwood et al.		
Gulf coast	(1978)	0.44	1.51
Texas			
Gulf coast	This paper	0.75	2.57

[1]Derived from their table 10 by computing the product of mean herd size (5.43) and mean herd density (0.0497).

to the total number of animals counted (9.3±2.0%) is about the same as previously reported (Leatherwood 1979).

Distribution and Behavior

As can be seen from Figures 1-3 the distribution of dolphin herds in the area was hardly homogenous. Some 28 herds (21%) of the total were sighted in the narrow Aransas Pass ship channels (mainly transect 1) and 211 (23%) of the animals counted were in these herds. (This marked difference in densities is discussed below.) Transect 18 across Matagorda Bay was another area of high dolphin density. While we noted only eight herds on this line they were relatively large and accounted for 14% of the dolphins sighted. In general, aside from the ship channels, the shoreward side of the barrier islands and locations close to the beach appeared to be favorable situations for *T. truncatus*, whereas sightings were rare in the middle of large bays.

When possible, the apparent behavior of the herds was coded as either traveling, playing, feeding, or resting. Of the 97 herds classified, about half (48.5%) were considered to be feeding. Side or upside down swimming by dolphins actively pursuing prey as reported by Leatherwood (1975) was frequently observed. This was particularly true in the shallow regions inside the barrier islands where Gunter (1954) reported that bottlenose dolphins frequently chase mullet, *Mugil cephalus*. Feeding appeared to be associated with herd size, for of the 17 herds composed of 15 or more individuals, 13 (76.5%) were considered to be feeding. The next most common behavior was "traveling," and 36 herds (37.1%) were assigned to that behavioral mode.

Perpendicular Sighting Distances and Sighting Cues

As previously indicated, in most cases we estimated the perpendicular distance from the plane's track to the sighted herd. In addition we also logged the nature of the observation which first alerted us to the presence of a dolphin herd, the "sighting cue" (Figure 5). During the field work, 11 different codes were used but these could be reduced to four classes: 1) surface perturbations such as mud trails or boils, scars, and splashes; 2) an animal's body seen below the water (most easily noted when the dolphins are rolling or swimming upside down and their contrasting light ventral surfaces are showing); 3) an animal's body, or part of it, or its condensed respiratory exhalation "blow" noted above the water surface; and 4) "cue uncertain or unnoted."

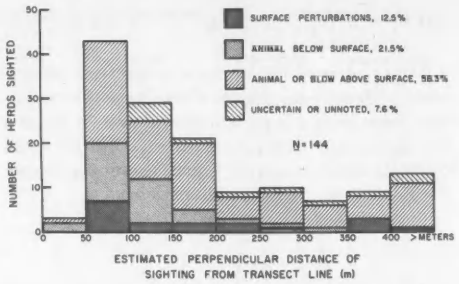

FIGURE 5.—Frequency distribution of estimated perpendicular distances of bottlenose dolphin herd sightings from transect lines on surveys 1-5, Port Aransas to Matagorda, Texas. Histograms are divided into the relative ratios of sighting cue classes.

The "animal above surface" cue was effective at all ranges and was the predominant sighting cue, accounting for 58.3% of all sightings (Figure 5). The "animal below surface" instigated 21.5% of the sightings, but was more important at ranges under 200 m, contributing 28 of the 96 sightings (29.2%) at these ranges, whereas, at ranges >200 m, only 3 of 48 sightings (6.2%) were signaled by this cue. As will be discussed later, the effectiveness of both underwater sightings and surface perturbations appeared to be vulnerable to weather conditions. Most questionable or unrecorded sighting cues occurred on the initial survey.

DISCUSSION

Possible Biases to Population Estimates

Several factors, both operational and analytical, influenced the results, in some cases prejudicing the counts upward and in others to lowering them. We first discuss two factors, effects of weather and inability to sight all herds, that tended to cause underestimates.

Relatively strong southwest winds (22-41 km/h) blew constantly for several days during the field operations. The wind's major effect on searching efficiency was not sea state, as is the case in the open ocean, for splashes were seldom the sighting cue, but rather the stirring of bottom materials into suspension creating large areas of highly tur-

bid water. On such days the only clear water was in the lee of barrier islands and headlands where the fetch was limited.

Increased turbidity limits the observer's chances of sighting underwater animals and noting mud boils and trails. For underwater animals, however, the overall effect on the number of sightings was tempered because submerged dolphins will frequently be spotted when they eventually surface. More important was the negative influence of high turbidity on the observer's ability to note surface signs. For example, on the two low-wind days 12 out of 68 (17.7%) sightings were cued by surface perturbations. In contrast, on the three medium to high-wind days only 8 of 83 (9.6%) of sightings were signaled by this cue. The effect was probably more important than those data indicate, for frequently the observer's attention was drawn to an area by subtle surface signs and then, if a dolphin's body showed at the surface, it was usually the second rather than the first cue that was logged. As stated earlier, we have reduced the effects of weather on the population estimates by excluding the results of survey 5, when the wind effects were extreme, from the density computations.

Regarding our inability to sight all herds, the supposition that all target animals will be seen is basic to the strip transect method (Eberhardt 1978). However, in terms of line transect theory (Seber 1973), which assumes that the herds will be randomly distributed, the frequency histogram of the estimated perpendicular sighting distances (Figure 5) gives strong evidence that one of these assumptions was incorrect, probably the former, as follows. First, only 3 of 144 sightings were made at under 50 m range. The aircraft's configuration which severly limits searching the water directly under and adjacent to the flight path was the major cause of this discrepancy. (A secondary factor was discomfort to the observer's neck caused by attempting to look down at a steep angle.) The only sightings made directly under or close to the track were when the aircraft was in a steep turn, and frequently herds were noted at moderate ranges when we were circling on a previous sighting. Secondly, the systematic decrease of the sighting frequencies from 50 to 200 m, suggesting a negative exponential curve, and the "tail" out to 400 m must at least in part reflect the inherent inefficiency of the observers to see beneath the water's surface at low angles or to detect relatively small, low-contrast objects at even moderate distances.

Three factors, dolphin movement, nature of the terrain, and observer experience, may have had mixed effects on the estimates, as follows.

Regarding effects of dolphin movement between the open Gulf of Mexico and the bay behind the barrier islands, it was originally planned that volunteer observers stationed adjacent to the passes would note the numbers and directional movements of bottlenose dolphins during the hours of the survey. However, a week's delay in starting the field work and the subsequent resumption of college classes following Easter vacation made it necessary to cancel that observational phase. At the termination of survey 4, however, we flew homeward just outside Matagorda Peninsula and Island. Outside Pass Cavallo at least 50 *T. truncatus* were seen lolling in small herds in and just outside the surf zone. These dolphins may have either been moving in from the Gulf or out of the bays, but their proximity to the beach and the pass indicates that there was frequent movement of dolphins between the two environments.

Factors of bathymetry of the bays and the nature of the terrain were not considered by the analysis. While *T. truncatus* were occasionally noted in shallow water just inside the barrier islands, extensive regions in the middle of the bays and in the shoreward areas were covered with a thin layer of water over sand and mud flats and there are numerous reefs and islands. Thus, within most of the 800 m swaths used to compute the density estimates there was territory that was not available to the dolphins that could legitimately be subtracted from the area searched. On the other hand, by multiplying the searched area by 5.76 (Equation (3)) to obtain an estimate of the total number of dolphins we were sometimes attributing dolphin habitat to dry land. This is particularly true for the Port Aransas ship channels that were limited to about 600 m width and were surrounded by large land areas.

We feel that observer experience possibly also biased the accounts. *Tursiops truncatus* herds appear to occupy a home range (Caldwell 1955; Shane 1977) and we frequently sighted herds that were of similar size and in the same approximate location of herds noted on previous surveys. The observers tended to concentrate their attention on these areas and thus searched them more efficiently in the latter surveys.

Despite the smallness of the herds, it was not easy to accurately count animals that were sometimes spread over a relatively large area, and in subgroups that only showed for brief periods at the surface. Obviously, accuracy of such counts will also improve with experience. However, by scoring a consensus opinion the judgment and bias of the most experienced observer probably carried more weight, and as a result we feel that in all cases the counts were conservative. Because of the experience factor we also think that, other influences being equal, the latter surveys were probably the more accurate.

Last, one factor, the "gerrymandered" lines of transects 1 and 2, clearly tended to influence the counts upward. Our rationale for altering the line of these transects was based on the desirability of obtaining data in an area for which baseline information already was available (Shane 1977). Unfortunately, the terrain was not ideal for transect sampling, and flying an east-west line over the ship channels would have resulted in gross underestimation of an area known to hold a relatively large number of dolphins.

Clearly, the results for transects 1 and 2 (23% of the animals sighted in only 6.6% of the total area) were strikingly different from those data for the rest of the transects. Estimated dolphin density for the ship channels was 2.633/km^2, some 4.25 times greater than the 0.619/km^2 estimated for transects 3-21 (Table 4). Based on these densities the total population estimate could be partitioned into 304 dolphins for the ship channels and 1,015 animals in the rest of the area. Shane's (1977) maximum estimate for the ship channel area for any month of the year was about 280, thus the two estimates are in reasonable agreement. We still feel, however, that there were some unresolvable problems with our survey methodology as it applied to the Aransas Pass ship channels, and that the soundest procedure was to lump the results from the minority area with those from the major region, as we have done.

Alternative Density Estimate

As previously discussed, the decrease in the number of dolphin sightings at increasing ranges of the herds from the flight path (Figure 5) indicated violation of strip transect theory assumption that all herds within the delineated area were sighted. Line transect theory (Seber 1973) provided an alternative method of analyzing the results. Because there were few observations in the 0-50 m increment, creating a marked gap in the frequency distribution, and the "tail" of the frequency distribution was truncated, in part because we limited observations to about 400 m range, our data were not strictly applicable to line transect theory, either. Despite these discrepancies, however, we obtained for comparative purposes a rough approximation of the level of bias by applying a simple modification of the so-called exponential estimator (Gates et al. 1968) which corrects for the gap in the 0-50 m frequency distribution interval as follows:

TABLE 4.—The basic terms and figures for comparing the estimated bottlenose dolphin density in two parts of the survey, the Port Aransas ship channels (transects 1 and 2) and rest of the area (transects 3 to 21).

Survey number (replicate)	Total no. of herds	Total no. of animals	Mean herd size ($\bar{h}_j$)	Herd density no./km^2 ($\hat{D}_j$)	Dolphin density (no./km^2) ($\hat{d}_j$)	Variance dolphin density (Var $\hat{d}_j$)
Transects 1 and 2						
1	5	41	8.20	0.2165	2.045	1.6005
2	8	35	4.38	0.3465	1.749	0.5162
3	8	84	10.50	0.3465	4.191	5.0629
4	7	51	7.29	0.3032	2.546	2.0490
Total	28	211				
Mean	7	52.6	7.59	0.3032	2.633	
SD	1.4	21.9	2.53	0.0613	1.090	
SE	0.7	10.9	1.27	0.0307	0.545	
SE[1]						0.8750
Transects 3 to 21						
1	31	134	4.32	0.0946	0.471	0.0121
2	28	225	8.04	0.0854	0.791	0.0350
3	21	125	5.95	0.0641	0.439	0.0133
4	25	221	8.84	0.0763	0.776	0.0552
Total	105	705				
Mean	26.3	176.3	6.79	0.0801	0.619	
SD	4.3	54.1	2.05	0.0130	0.190	
SE	2.1	27.0	1.03	0.0065	0.095	
SE[1]						0.0980

[1]From Equation (13).

$$\hat{d} = \frac{n}{2L(\bar{Y} - 0.05)} \quad (14)$$

where $\hat{d}$ = estimated dolphin density,
n = total number of dolphin sightings,
L = length of the track line in km,
Y = mean perpendicular sighting distance (minus the 50 m gap).

These calculations gave a density estimate for herds of 0.28/km² compared with 0.095 for the strip transect method (Table 2), evidence that the latter method may have underestimated the dolphin density by about a factor of 3.

In conclusion, the relatively few sightings in the 0-50 m perpendicular distance interval and the exponential decrease in sightings at ranges >100 m, strongly indicate violation of the strip transect assumption that all herds within the delineated strip were noted. If this is true then the population has been underestimated to some degree, although the inclusion of transects 1 and 2 would tend to compensate for this. Conversely, one assumption of line transect theory is that the targets are randomly distributed. We found, however, that the distribution of the dolphin herds was strongly nonrandom. This factor may have caused an upward bias to those calculations, but the precise impact of this violation is presently unclear. These questions cannot be resolved until further surveys are done simultaneously with adequate "ground truth" counts.

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ENERGETIC SIGNIFICANCE OF CHANGES IN SWIMMING MODES DURING GROWTH OF LARVAL ANCHOVY, *ENGRAULIS MORDAX*

DANIEL WEIHS[1]

ABSTRACT

The swimming behavior of larval northern anchovy, *Engraulis mordax*, in the first few days after hatching is different from the intermittent beat-and-glide mode used by older larvae and later stage fish. It is shown mathematically that the bursts of continuous swimming typical of these yolk-sac larvae is the more efficient form of locomotion at this stage, because of their small size. This advantage changes as the larva grows out of the size range in which water viscosity is the dominant factor (small Reynolds number). When the larva reaches a length of 5 mm, typical Reynolds numbers are such that intermittent swimming gradually becomes the more economical mode, and this mode is dominant when the larvae reach 15 mm. These analytical results compare well with observed behavioral changes.

Swimming behavior of the northern anchovy, *Engraulis mordax*, changes dramatically during growth in the larval stage (Hunter 1972). At hatching, the motion of yolk-sac larvae consists of bouts of continuous, very energetic swimming. This behavior persists for the first 3-4 days of growth, changing to beat-and-glide swimming at the close of the yolk-sac period. The beat-and-glide mode is then retained during the rest of the fish's life.

Intermittent swimming, or beat and glide, is an efficient mode of locomotion for adult fish, enabling increases by a factor of two or more in the range achieved for a given energy expenditure (Weihs 1974). The problem addressed in the present paper is whether the changes in swimming behavior mentioned above also have an energy-saving function. The energetic advantage of intermittent swimming may not exist during the early life stages of fishes because of the importance of viscous effects on small organisms. This study includes setting up a theoretical framework for the analysis of energetics of swimming during the various stages of the fish's life history. The forces and energy required for swimming in the continuous and intermittent modes are then calculated and compared at different stages of larval development. These stages are hydrodynamically distinguished by the nondimensional Reynolds number, Re, which is a function of both length and speed. The value of the Re defines the relative importance of viscous and inertial effects on the hydrodynamic resistance to motion.

THEORETICAL MODEL

Consider a fish swimming in a straight line at constant depth. We shall assume the fish to be neutrally buoyant so that the only forces acting are in the horizontal plane. Fish of negative buoyancy can be included in the following analysis by equating the excess weight of the fish in water (which is usually not more than 6% of its weight in air) and lift forces produced on the body and fins. However, this is not directly relevant to the present discussion as these forces are perpendicular to the plane of motion, and shall therefore be left out for simplicity.

Returning to the horizontal plane, the forces acting are the thrust applied by the fish, T, and the drag on the fish, D, acting in the opposite direction. The drag is a combination of viscous drag due to friction and form drag, which also is an indirect result of the friction caused by areas over which the flow is separated from the fish body. The drag force can be written (Hoerner 1965) as

$$D = \frac{1}{2}\rho A C_D u^2 \qquad (1)$$

where ρ is the water density; A the frontal area (seen in frontal projection); C_D a nondimensional drag coefficient dependent on shape, roughness, and other factors to be discussed below; and u the relative velocity between the fish and the water

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some distance away, which is not disturbed by the fish's passage.

The drag coefficient C_D has been found experimentally to be a similar function of Re for various shapes. Thus, for all shapes tested (Hoerner 1965, chapter 3), the coefficient C_D is a decreasing function up to Re 200-300, being a constant for larger Re up to the turbulent regime which starts at about Re = 500,000, where a new, lower, constant value is obtained. Thus when Re>200, hydrodynamic drag becomes proportional to the velocity squared, as the other factors in Equation (1) do not change for a fixed body.

The Re>200 regime was examined by the author (Weihs 1974) previously and will therefore be mentioned here for comparisons only. When Re<200, two main regimes are observed, that of Re<10 and 10<Re<200. The low Re range, in which velocity plays a much more important role than the inertial (acceleration) force effects, has $C_D \propto \mathrm{Re}^{-1}$. Strictly speaking, this regime ends when Re = 1, but experiments have shown that this relationship can be applied up to Re = 10 with good accuracy. Vlymen (1974) actually used this relationship at Re = 30, where C_D, estimated by the low Re formula, still is within 10% of the exact value, for his analysis of larval anchovy swimming. The remaining range is a transition regime where C_D gradually changes from the low Re form to the high Re ($C_D \propto \mathrm{Re}^0$) form.

As continuous swimming in anchovy larvae is observed mainly in the yolk-sac stage (2.8-5 mm long), the low Re regime is relevant. Thus, Re = 8 corresponds to a 3 mm long larva moving at 3 mm/s, and a 5 mm long larva, moving at 5 mm/s, experiences a Re<30.

Applying the relationship for low Re ($C_D \propto \mathrm{Re}^{-1}$), Equation (1) can be written

$$D = \frac{1}{2}\rho ACu \tag{2}$$

where C is a numerical constant depending on the shape.

When a fish is actively swimming by means of body and fin oscillations, the drag force is affected, both through the increase in frontal area A, and through the change in the numerical coefficient C. Thus, for example, $C = 20.37$ for a disc moving in a direction normal to its plane, and is equal to 13.6 when moving parallel to its plane. Experimental data collected by Webb (1975) show that the drag coefficient for fish swimming at high Re can be up to four times that of a rigidly gliding fish. For the low Re regime considered here, the increase in drag coefficient caused by swimming motions does not exceed a factor of 2, for a long slender body (Wu et al. 1975). This increase is written as

$$D_s = \frac{1}{2}\rho AC\alpha u \equiv \alpha Ku \tag{3}$$

where α is the ratio of swimming to gliding drag and the subscript s stands for active swimming. The equation of motion for fish, while actively producing a thrust T is

$$T = m\frac{du}{dt} + \alpha Ku \tag{4}$$

where m is the fish mass (slightly augmented by the added mass at higher Re), and K is defined in Equation (3).

The energy (E) required to traverse a distance L within time τ is

$$E = \int_0^{\tau} T\,u\,dt. \tag{5}$$

There is no available information on the dependence of propulsive efficiency on swimming speed for larval anchovy, so that we have to perform the calculations on the energy required, and not the energy actually expended by the fish. However, for comparison of different swimming modes, these are equally applicable.

The purpose of the present study is to compare the effectiveness of continuous and intermittent swimming of larval fish so that we start by finding the energy, E_c, required for swimming at constant speed U_c over the same distance L. From Equation (5),

$$E_c = T_c U_c \tau = T_c L \tag{6}$$

where the subscript c stands for continuous swimming. Defining the energy expenditure per unit distance as $\bar{E} = E/L$ we obtain, by applying also Equation (4),

$$\bar{E}_c = T_c = \alpha KU_c. \tag{7}$$

Intermittent swimming, on the other hand, requires energy only during the beating part of the cycle so that the total energy for one beat-and-glide cycle is described by

$$E_v = \int_0^{t_1} T\,u\,dt = \int_0^{t_1} \left(mu\frac{du}{dt} + \alpha Ku^2\right) dt \tag{8}$$

where t_1 is the time spent in active swimming during the cycle. In order to integrate Equation (8) we have to obtain the functional dependence of u on the time t. This is done with the aid of Equation (4). Taking the thrust applied to be constant (T_0), Equation (4) can be solved in closed and general form. It was previously shown (Weihs 1974) that constant thrust production is the most efficient procedure so that we can use this assumption here, recognizing that any other behavior will probably be more wasteful in terms of energy. After some rearrangement, Equation (4) is

$$\frac{du}{dt} + \frac{\alpha K}{m} u - \frac{T_0}{m} = 0 \tag{9}$$

with boundary condition

$$u = U_i \text{ at } t = 0 \tag{10}$$

where U_i is the initial velocity at the beginning of the beat phase, which is equal to the speed at the end of the gliding phase. The solution is

$$u = (U_i - U_0) \exp\left(-\frac{\alpha K}{m} t\right) + U_0 \tag{11}$$

where $U_0 = T_0/K$ is the final velocity which the larva would attain if the beating phase were sustained for a long enough period. U_0 is higher than the final speed actually obtained during the beat phase U_f. Substituting Equation (11) into Equation (8) and integrating, recalling that the speed at t_1 is U_f, we have

$$E_v = mU_0 (U_0 - U_f) + \alpha K {U_0}^2 t_1. \tag{12}$$

To find t_1, we substitute U_f in Equation (11) with $t = t_1$ and obtain, after algebraic reduction

$$t_1 = \frac{m}{\alpha K} \ln \frac{U_0 - U_i}{U_0 - U_f} \tag{13}$$

so that the energy required during one beat-and-glide cycle is

$$E_v = m{U_0}^2 \left[\left(1 - \frac{U_f}{U_0}\right) + \ln \frac{1 - \dfrac{U_i}{U_0}}{1 - \dfrac{U_f}{U_0}} \right]. \tag{14}$$

The energy per unit distance crossed during one cycle in intermittent swimming is

$$\bar{E}_v = \frac{E_v}{l_1 + l_2} = \frac{E_v}{U_i \bar{\tau}} = \frac{E_v}{U_i (t_1 + t_2)} \tag{15}$$

where l_1, and l_2 are the distances crossed during beating and gliding phases, respectively. The sum of l_1 and l_2 is taken to be equal to the continuous swimming speed U_c multiplied by the total cycle time, as we compare energy required for crossing the same distance $l_1 + l_2$. Thus, U_c is also the average velocity during the whole intermittent swimming cycle

$$U_c = \frac{l_1 + l_2}{t_1 + t_2}. \tag{16}$$

To compare energy expenditure in intermittent and continuous swimming, we define a ratio S

$$S = \frac{\bar{E}_v}{\bar{E}_c} = \frac{E_v}{\alpha K {U_c}^2 (t_1 + t_2)} = \frac{E_v (t_1 + t_2)}{\alpha K (l_1 + l_2)^2}. \tag{17}$$

Intermittent swimming is more efficient only when the numerical value of S is less than unity. To calculate values of S we need explicit expressions for l_1, l_2, t_1, and t_2. The beat phase velocity has already been found, Equation (11), so that l_1 is easily obtained by integration, using t_1, Equation (13), as the upper bound

$$l_1 = \frac{m}{\alpha K} \left[U_0 \ln \frac{U_0 - U_i}{U_0 - U_f} - (U_f - U_i) \right]. \tag{18}$$

The gliding phase of intermittent swimming is described by

$$m \frac{du}{dt} + Ku = 0 \tag{19}$$

which is obtained from Equation (4) when no thrust is applied, and gliding drag is experienced by the fish. The relevant initial condition is

$$u = U_f \text{ when } t = 0 \tag{20}$$

and the speed is

$$U = U_f \exp\left(-\frac{K}{m} t\right) \tag{21}$$

with the time spent gliding t_2 obtained from the fact that at t_2 the speed is back to U_i. After some reshuffling

$$t_2 = \frac{m}{K} \ln \frac{U_f}{U_i} . \quad (22)$$

Integrating Equation 20 gives l_2

$$l_2 = \int_0^{t_2} U_f \exp\left(-\frac{K}{m} t\right) dt = \frac{m}{K}(U_f - U_i) . \quad (23)$$

To nondimensionalize, we now divide all velocities by U_0. Substituting Equations (13), (14), (18), (22), and (23) into S (Equation (17)) and simplifying results in

$$S = \frac{\left[(1-\bar{U}_f) + \ln \frac{1-\bar{U}_i}{1-\bar{U}_f}\right]\left[\ln \frac{1-\bar{U}_i}{1-\bar{U}_f} + \alpha \ln \frac{\bar{U}_f}{\bar{U}_i}\right]}{\left[(\alpha-1)(\bar{U}_f-\bar{U}_i) + \ln \frac{1-\bar{U}_i}{1-\bar{U}_f}\right]^2} \quad (24)$$

where the line over the speeds signifies values divided by U_0. The ratio S serves now as a quantitative criterion, showing which mode of swimming is more efficient. The advantages of the comparison approach are now clear, as the only parameter specific to the fish is α which, as mentioned before, can vary between 1 and 2 only. All other factors, such as fish mass, frontal area, and the numerical coefficient of drag, have cancelled out, dropping many of the uncertainties of such calculations.

Results and Discussion

Equation (24) is now studied for various values of the parameters involved. As mentioned before, the numerical value of S indicates the relative efficiency of intermittent and steady swimming. When $S>1$ beat-and-glide swimming is more costly. The three variables appearing in S are bounded by well-defined limits, which makes the parametric study of Equation (24) easier. The nondimensional "final" velocity, at the end of the beat phase, is limited by $0<\bar{U}_f<1$ as U_0 is the highest velocity obtainable by the animal (see Equation (11)) under present conditions. By definition, $0<\bar{U}_i<\bar{U}_f$. The yolk-sac larvae and later stage larvae are combinations of elongated and round shapes so that the limits of α are $1 \leq \alpha \leq 2$. The range of values of α is obtained from the fact that for elongated (fish) bodies, the ratio of drag in normal motion to resistance to tangential relative motion does not exceed 2 in the viscous domain. Only some sections of the fish bodies are in pure normal motion (perpendicular to the local flow direction), consequently the average ratio is always <2.

It is also clear that the larger the numerical value of α, the larger the possible gains by means of intermittent swimming, because the drag when actively swimming is proportionally greater than while gliding so that breaks in the swimming phase will be more advantageous. Therefore, we first take $\alpha = 2$ as a reasonable upper limit. Figure 1 shows the results of such calculations. The coordinates are the energy ratio S versus the normalized average velocity U_c. The calculations were performed for different values of the final

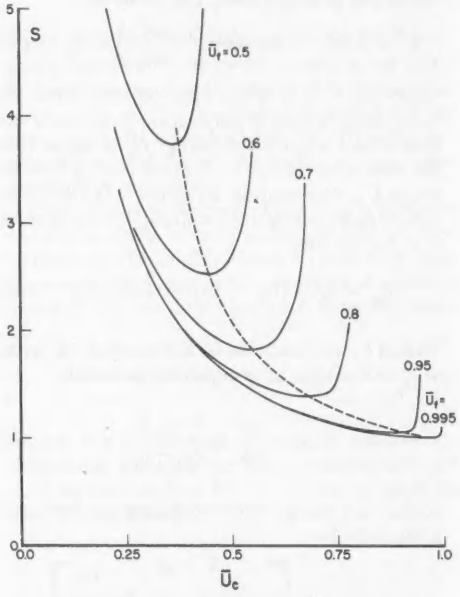

FIGURE 1.—The ratio of energy required per unit distance S for intermittent swimming and continuous swimming respectively, versus the nondimensional average speed $\bar{U}_c$, for various values of speed at the end of the beating phase, $\bar{U}_f$. All speeds are normalized by the speed U_0 attained at maximum sustained thrust T after a long time. Dashed line shows locus of minimal energy ratio at different $\bar{U}_f$. Ratio of swimming to gliding drag α = 2.

velocity U_f, varying the initial velocity U_i to obtain different average speeds.

The main result of this Figure is that S is always >1, i.e., for the speeds and sizes at which viscous effects dominate continuous swimming is always more efficient. This calculation is based on the relation $C_D \propto \mathrm{Re}^{-1}$ and is therefore valid for Re up to 10. Larval anchovy tend to swim at speeds of about 0.8 body length/s (Hunter 1972) when swimming intermittently. Thus the Re typical of 3-day-old larvae whose length (Zweifel and Hunter[2]) is about 4 mm at 18° C is also about 10. At age 3 days, larvae spent <20% of the time swimming intermittently, but 2 days later (Hunter 1972, fig. 1) about 90% of the time is spent in beat-and-glide motion. This level of intermittent swimming is retained thereafter. This sharp change coincides with the time the animal "grows out" of the viscous regime (the Re is essentially proportional to fish length squared), e.g., when the larvae is 5 mm long, the Re is 20.

Recalling that at high Re, beat-and-glide swimming is the more efficient motion (Weihs 1974), the energy saving obtained is probably one of the reasons for the observed change in swimming behavior.

The fact that the average continuous speeds are much higher also results in savings of energy. For a 3-4 mm long larva, swimming at over 1 cm/s brings it again to Re of over 20, so that the drag coefficient is smaller, and some coasting at the end of the bout of continuous swimming is possible. At lower Re, in the purely viscous regime, no coasting is possible as the inertial effects are negligible and motion ceases immediately when oscillations stop. It is therefore advantageous for the fish, for hydrodynamic reasons, to swim continuously during the first few days of the larval phase, changing to beat-and-glide swimming later on. It should be noted here that the present calculations and data are for a water temperature of 17°-18° C. Both viscosity of water and the growth rate of larvae (see footnote 2) depend on the temperature, so that data collected under different ambient conditions might lead to a later (or earlier, if the temperature is higher) change of swimming mode.

Further examination of Figure 1 shows that for each terminal velocity in the beating stage there is a value of $\bar{U}_c$ for which the ratio S attains a minimum (marked by the dashed line). The value of this minimum approaches unity and the curves become more shallow as $\bar{U}_f$ increases. Thus, if an anchovy larva swims intermittently at low Re, it should do so at high average speeds, so that the energy penalties incurred due to swimming in the beat-and-glide mode are minimal.

Figure 1 also shows that the lowest penalties for using intermittent swimming are obtained when $\bar{U}_f$ approaches unity, for the whole range of average speeds. Therefore, the value $\bar{U}_f = 0.995$ was chosen for calculations of the effect of varying α (the ratio of swimming to coasting drag). These appear in Figure 2, where the dependence of S on $\bar{U}_c$ is shown. The range of values of α to be expected in nature is described by the shaded area, showing as expected that the smaller the α the more advantageous is continuous swimming. When $\alpha>2$, which can only happen at higher Re, a range of values of $\bar{U}_c$ and $\bar{U}_f$ exists where S is smaller than unity, i.e., intermittent swimming is more efficient. This is shown by the dashed curve on Figure 2 where for $\bar{U}_f = 0.995$ and $0.79<\bar{U}_c<1$, $S<1$. This curve will be discussed later, in reference to the transition region between the low and high Re domains.

The results discussed above all dealt with the low Re range. For comparison, we now show the equivalent energy ratio for high Re, i.e., the domain relevant to larger larvae as well as adult anchovy (>15 mm long). The results presented

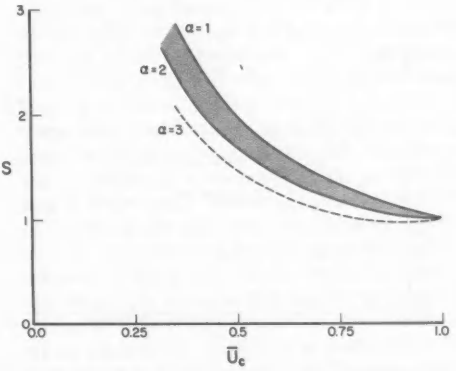

FIGURE 2.—Influence of changes in ratio of swimming drag to gliding drag α on the energy ratio S, versus nondimensional average speed $\bar{U}_c$. Shaded area is the range of possible α at low Reynolds numbers. $\bar{U}_f = 0.995$ (See Figure 1 for definitions).

[2]Zweifel, J. R., and J. R. Hunter 1978. Temperature specific equations for growth and development of anchovy (*Engraulis mordax*) during embryonic and larval stages. Unpubl. manuscr., 13 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

stem from calculations based on the analysis in Weihs (1974). The ratio of energy per unit distance traversed in intermittent swimming to that of continuous swimming at the same average speed R, can be shown to be, in present notation,

$$R = \frac{\tanh^{-1}\left(\frac{\bar{U}_f-\bar{U}_i}{1-\bar{U}_i\bar{U}_f}\right)\left[\tanh^{-1}\left(\frac{\bar{U}_f-\bar{U}_i}{1-\bar{U}_i\bar{U}_f}\right)+\alpha\left(\frac{1}{\bar{U}_i}-\frac{1}{\bar{U}_f}\right)\right]}{\left[\ln\left\{\cosh\left[\tanh^{-1}\left(\frac{\bar{U}_f-\bar{U}_i}{1-\bar{U}_i\bar{U}_f}\right)\right]+\bar{U}_i\sinh\left[\tanh^{-1}\left(\frac{\bar{U}_f-\bar{U}_i}{1-\bar{U}_i\bar{U}_f}\right)\right]\right\}+\alpha\ln\frac{\bar{U}_f}{\bar{U}_i}\right]^2}. \quad (25)$$

The computed values of R, for $\alpha = 2$, appear in Figure 3. Each full line describes the values of R for a given $\bar{U}_f$ as a function of the average velocity U_c. Each of these curves ends at $\bar{U}_c = \bar{U}_f$ and, in a similar manner to Figure 1, has a minimum for a lower value of U_c. Here, however, all curves have a large section in the range $R<1$, i.e., intermittent swimming is more efficient. In fact, the slower the average velocity, the higher the possible gains, as shown by the dashed line which is the locus of lowest values of R as a function of $\bar{U}_c$. As already mentioned in Weihs (1974), this curve goes monotonously from unity at $\bar{U}_c = 1$ (continuous swimming by definition) to $1/\alpha$ at $U_c \to 0$. One can therefore predict that fish species using the anguilliform swimming mode (Breder 1926) will find intermittent swimming relatively more efficient than carangiform swimmers as α is greater for anguilliform swimming in which most of the body is oscillated. Another result is that for greatest gains, the average speed during the whole beat-and-glide should be as low as possible, with small differences between $\bar{U}_i$ and $\bar{U}_f$.

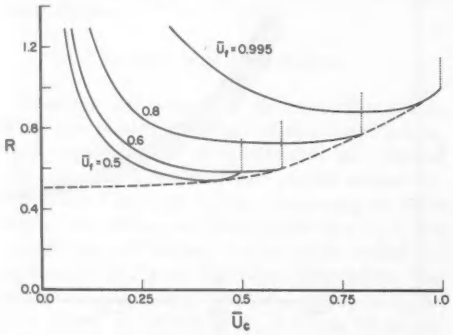

FIGURE 3.—The ratio of energy required per unit distance R, for intermittent and continuous swimming at high Reynolds numbers, respectively, versus nondimensional average speed U_c. Dashed lines shows locus of minimum values of R attainable as a function of $\bar{U}_c$. See Figure 1 for definitions.

Anchovy, which swim in the anguilliform mode, fulfill both these predictions as adults and more mature larvae usually swim by means of a single beat followed by a long glide, so that 1) $\bar{U}_i$ and $\bar{U}_f$ are not too different and 2) $\bar{U}_c$ is rather low.

Having examined the low and high Re domains, where the drag coefficient is porportional to the reciprocal of Re, and constant, respectively, we now look at the transition regime between them. Based on average swimming speeds of 0.8 body length/s, larvae will be in this regime when they are from 5 to 15 mm in length. Analysis of the forces and energy is much more complicated here because the hydrodynamic drag is

$$C_D \propto \mathrm{Re}^{-\beta} \quad (26)$$

where β is not constant, but itself is a function of both Re and body shape. This results in Equation (4) taking the form

$$T = m\frac{du}{dt} + \alpha K u^{2-\beta} \quad (27)$$

a differential equation that has to be solved numerically when β is not zero or one (the two cases discussed previously). While this in itself is a relatively straightforward task, the generality and accuracy of the previous solutions is immediately lost as numerical values for the mass and K have to be included. K especially is known very inaccurately as it includes the numerical drag coefficient and the frontal area (which varies at different speeds and times). The setting of β is even more problematical as it depends on the instantaneous swimming speed in an empirical manner (which

is, however, not known at the present time), thus changing during the beat-and-glide cycle. No single value may therefore be taken to describe a given beat-and-glide behavior and an average value has to be used. This adds greatly to the inaccuracy as β is an exponent. Bearing especially the latter factor in mind, no smooth curves of the type appearing in Figures 1-3 can be expected.

In order to try and make clear how the transition regime influences the energetics of swimming, in spite of the difficulties mentioned, curves such as those from Figures 1 and 3 are reproduced in Figure 4. The purpose of this Figure is to show that by using the correct nondimensional description, curves for the viscous and nonviscous regimes can be compared. Both the dashed and full curves have similar shape, going to infinity for $\bar{U}_c \rightarrow 0$ and having a minimum at the higher values of $\bar{U}_c$, the values increasing again for $\bar{U}_c \rightarrow \bar{U}_f$. One must recall that the absolute speeds and sizes are very much different for the two cases, this resulting from the difference in U_0, the maximum sustained speed. U_0 is much larger for the full curves. The dashed curves have $\beta = 1$ while the full lines are for $\beta = 0$. Therefore, calculations at any intermediate values of β are expected to fall between them.

Some calculated values appear in Figure 4, for two values of average β. While they show the expected behavior, their actual values are, as mentioned before, unreliable, because they are based on rough estimates of various coefficients which do not have to be made when $\beta = 0$ or 1. These computations are to be taken only as an indication that the expected gradual transition actually occurs and are not to be used for actual calculations.

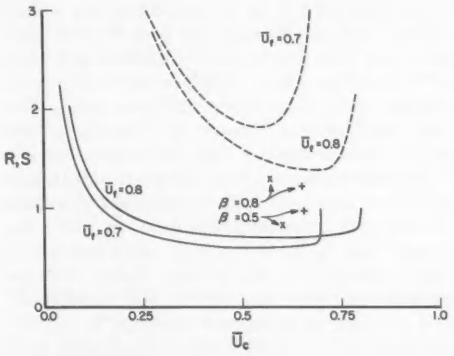

FIGURE 4.—Energy ratio versus nondimensional speed at various Reynolds numbers. Dashed lines show the low Reynolds number (viscous) regime, full lines are for high Reynolds numbers (boundary layers) and, ×, + are at intermediate Reynolds numbers, for $\bar{U}_f = 0.7$ and $\bar{U}_f = 0.8$, respectively. See Figures 1 and 3 for other definitions.

Keeping these limitations in mind, one can tentatively come to the conclusion that the intermediate Re regime is one of gradual transition. The advantage of beat-and-glide intermittent swimming becomes more and more significant as the larva grows, after the 4th day after hatching.

This conclusion can be strengthened, in a roundabout manner, by a different approach. The ratio of swimming to gliding drag for a given animal is 2 in the low Re regime, and up to 4 for high Re. Therefore taking a higher value of α for the viscous domain calculations can indicate, in a different manner, the trend of results when increasing Re. This appears in Figure 2, where the dashed line stands for $\alpha = 3$. It can be seen that this curve is intermediate between typical curves for the viscous (Figure 1) and inertial regimes (Figure 3).

CONCLUDING REMARKS

It was demonstrated in the previous section that the change in swimming style observed when anchovy larvae reach the age of 4-5 days is correlated with the passage of the animal from the highly viscous regime to the boundary layer regime. My calculations show that this behavioral change is an adaptive energy sparing mechanism. When the larva is <5 mm long, it can only progress by actively swimming as the enhanced effect of viscosity will bring it to a rapid halt when coasting. The yolk-sac, which still exists as a spherical protrusion, increases the drag even further at this stage. The drag coefficient here is inversely proportional to the velocity so that any low-speed motion is very costly in terms of energy. As a result, interspersing coasting and accelerating is not an efficient way of progressing. When the larva is larger (>5 mm) and moving faster, viscous effects are concentrated in a thin layer surrounding the fish and the influence of speed and shape on drag changes. At this stage, it is shown that intermittent motion is the more efficient for fish species such as anchovy which swim in the anguilliform mode. Intermittent motion is much less efficient for carangiform swimmers at all sizes (Weihs 1974) which may explain why species such as mackerel swim continuously at all phases of life.

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AN ANTIPREDATION MECHANISM OF THE POLYCHAETE *PHYLLODOCE MUCOSA* WITH NOTES ON SIMILAR MECHANISMS IN OTHER POTENTIAL PREY[1]

ROBERT S. PREZANT[2]

ABSTRACT

The polychaete *Phyllodoce mucosa* exhibits an antipredation response via the extrusion of a repulsive mucoid secretion. The mucus, secreted by large glandular regions of the dorsal and ventral parapodial cirri, prevents immediate ingestion of the worm by several species of small or juvenile fish. A sipunculid, *Phascoleopsis gouldi*; a nemertean, *Lineus ruber*; and a large flatworm, *Stylochus zebra*, are also distasteful to some potential predators. Antipredation responses found in some organisms may play an important role in regulating benthic community dynamics by mediating the feeding habits of certain predators during at least some stage of their development.

Feeding habits of many species of fish have been well established, but few studies have extended analyses beyond stomach contents. Results of such research frequently lead to labeling food found in the stomach as "preferred" (Onyia 1973; Smith and Daiber 1977). Reports of selective feeding behavior based mainly on stomach contents reveal the major types of food eaten by a fish but do not add substantially to our understanding of the interactions between predator and prey.

Ivlev (1961), discussing selective feeding by fishes, included the role of "constitutional defenses" of potential prey species as a mechanism which may contribute to predatory selectivity. Selectivity in food thus entails not only "preference" but avoidance of specific potential food items (Berg 1979). Bakus (1966) considered the possible role of antipredatory responses by some tropical reef inhabitants. He noted that several members of a reef community that are not readily able to retreat into the security of a coral crevice or not naturally protected by skeletal armor are either poisonous, venomous, or distasteful to predators. Acidic secretions from epidermal glands of some opisthobranch gastropods (Graham 1957; Thompson 1960, 1969) and some nemerteans (Gibson 1972) function as predatory deterrents. In view of the fact that predation is a well established cause of quantitative changes in a population of prey species, the ability of some members of a community to thwart extensive predatory cropping by using inherent protective devices may also affect community structure.

An accurate picture of community dynamics demands a closer examination of direct interactions between potential prey and predatory species. A start in this direction has been made on a limited number of fish. Hynes (1950), Tugendhat (1960), and Beukema (1968) examined some of the behavioral feeding patterns of the threespine stickleback, *Gasterosteus aculeatus*. They found that selective feeding of the stickleback is influenced by degree of satiation and palatability of food. This may have implications extending into the natural environment with regard to seasonal, predatory, or man-induced changes in community structure. In food-limited situations "selectivity" may decrease. The presence of a predatory deterrent in an organism may thus be functionally operative only in a nonstressed community with nonstarved predators.

Polychaetes often dominate marine benthic communities (Sanders et al. 1965) and many bottom feeding fish eat substantial quantities of these worms (Qasim 1957; Nikolsky 1963; Kislalioglu and Gibson 1977). Obscurance of taxonomic characters due to digestion often prevents identification of prey to species, so food items tend to be listed in terms of higher taxonomic levels (Hynes 1950; Kneib and Stiven 1978). This is especially true for soft bodied prey organisms and means that accurate feeding records are often nonspecific and possibly biased relative to the researcher's taxonomic expertise.

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Phyllodocid polychaetes secrete copious amounts of mucus when irritated (Fauchald 1977). Pettibone (1963) briefly noted that the mucoid secretion of *Phyllodoce maculata* may be offensive to predators. Preliminary observations of *P. maculata* and *P. mucosa* (Prezant 1975, unpubl. data) have confirmed that an epithelial, mucoid secretion acts as an antipredatory mechanism against at least one species of fish, the rock gunnel, *Pholis gunnellus*.

The present study extends these observations by quantitative experiments on behavioral interactions of *Phyllodoce mucosa* with several species of small or juvenile fish, and examines the possible defensive mechanism of this polychaete. Initial observations concerning antipredatory mechanisms in the phyllodocids *Eumida sanguinea* and *P. maculata*, the large flatworm *Stylochus zebra*, the sipunculid *Phascoleopsis gouldi*, and the nemertean *Lineus ruber* are also reported.

METHODS

Phyllodoce mucosa (Phyllodocidae) was collected in late August 1978 in Nahant Bay, Mass., by epibenthic sled from a fine sand substratum at a depth of about 17 m. *Eumida sanguinea* and the orbiniid *Scoloplos fragilis* were collected intertidally from Henlopen Flat, Lewes, Del., in early September 1978. *Scoloplos fragilis* was used as a control in the behavioral experiments because, despite its overall gross similarity to phyllodocids (i.e., long, thin worms of similar proportions), *S. fragilis* produces considerably less external mucus than *P. mucosa*. Worms were maintained in separate finger bowls on a running seawater table at 17° C and 32‰ salinity.

Fish used in behavioral experiments (Table 1) were collected in July 1978 and allowed to acclimatize for 30-60 days in separate compartments on the seawater table. During acclimatization, the fish were fed a variety of foods from a widemouthed glass pipette. Foods included bits of fresh blue mussel, *Mytilus edulis*; and American oyster, *Crassostrea virginica*; live tubificid oligochaetes, *Tubifex* spp.; brine shrimp, *Artemia marina*; and, infrequently, frozen brine shrimp.

Phyllodoce mucosa, typically found on fine sand substrata from low water to depths over 500 m, ranges from Labrador to Mexico (Pettibone 1963) thus geographically overlapping with all fish species used in this study (Table 1).

Since this research dealt principally with the inability of certain predators to eat *P. mucosa*, it was important to insure that the fish used would actively feed throughout the experimental period. Accordingly, several other species of polychaetes

TABLE 1.—The range, habitat, food habits, and collection sites of the species of fish used in the feeding experiments. The last column lists the test organisms offered to fish. Quantitative results are available only for *Phyllodoce mucosa*. Range, habitat, and feeding habit data for the fish are from Hildebrand and Schroeder (1928), Bigelow and Schroeder (1953), Chao and Musick (1977), and Kneib and Stiven (1978).

Fish species	Range and habitat	Feeding habits	Fish collection site	Test organism
Atlantic silverside, *Menidia menidia*	Nova Scotia to northern Florida; often over sandy or gravelly shores	Small crustaceans and molluscs, annelids, small fish, eggs, and plant material	Lewes Beach, Lewes, Del.	*Phyllodoce mucosa* *Scoloplos fragilis*
Weakfish, *Cynoscion regalis*	Nova Scotia to Florida; shallow coastal waters in summer	Fish, crabs, amphipods, mysids, shrimp, molluscs, annelids	Lewes Beach	*P. mucosa* *Phascoleopsis gouldi* *S. fragilis*
Windowpane flounder, *Lophopsetta maculata*	Gulf of St. Lawrence to South Carolina; sand bottoms from low water to 50 m	Mobile prey such as mysids, fish, shrimp, errant polychaetes	Lewes Beach and near Delaware Bay mouth at 18 m	*Phyllodoce mucosa* *Eumida sanguinea* *S. fragilis*
Sheepshead minnow, *Cyprinodon variegatus*	Cape Cod to Mexico; shallow waters of inlets and bays; salt marshes	Mobile epifauna including annelids	Lewes Beach	*P. mucosa* *S. fragilis*
Mummichog, *Fundulus heteroclitus*	Labrador to Mexico; shallow coastal waters especially salt marshes	Omnivorous (at least when >30 mm) including small crustaceans, annelids, and carrion	Canary Creek, Lewes, Del.	*P. mucosa* *Phascoleopsis gouldi* *S. fragilis*
Threespine stickleback, *Gasterosteus aculeatus*	Labrador to Virginia; salt and fresh waters	Small invertebrates, fish fry, eggs	East Point, Nahant, Mass., tide pool	*Phyllodoce mucosa* *S. fragilis*
Striped sea robin, *Prionotus evolans*	Gulf of Maine to South Carolina; coastal bottom dweller	Crustaceans, molluscs, annelids, small fish	Near Delaware Bay mouth at 18 m	*Stylochus zebra* *Phascoleopsis gouldi* *Lineus ruber*
Rock gunnel, *Pholis gunnelus*	Hudson Strait to Delaware; generally on rocky bottoms from low water to over 200 m	Molluscs, crustaceans, annelids	East Point, Nahant tide pool	*Phyllodoce mucosa* *P. maculata* *Nephtys incisa*

were fed to the fish before and following behavioral experiments. These worms, which were from various size classes, included: *Spio filicornis* (Spionidae) and *Nephtys incisa* (Nephtyidae) collected from Nahant Bay; and *Glycera americana* (Glyceridae), *Nereis virens* (Nereidae), *Scolecolepides viridis* (Orbiniidae), and *Hydroides dianthus* (Serpulidae) collected from Henlopen Flats.

The feeding behavior of each species of fish, excluding *Prionotus evolans* and *Pholis gunnellus*, was tested quantitatively with *Phyllodoce mucosa* and *Scoloplos fragilis*. Fish were starved for 24-48 h prior to testing. An individual fish was then placed in a separate 4 l glass aquarium or in a small compartment on the seawater table and allowed to acclimate for 60 min prior to experimentation. Each test session was composed of two sets of observations separated by a 5-min interval. A set consisted of five 1-min trials each separated by a 2-min interval. The trials entailed repeated exposure of randomly chosen worms to potential predation by each fish by dropping the worm from a widemouthed glass pipette in close proximity to the head of the fish. Since the fish were previously fed from a pipette, they showed no hesitation in accepting potential food items delivered in this manner. Following release from the pipette, several possible combinations of behavioral responses of the fish were noted: 1) ingestion of the worm, 2) rejection of the worm following an active attempt at ingestion, 3) presence or absence of investigations of the worm by the fish (investigation is defined here as an obvious "enticement" of the fish to the worm without an attempt at ingestion), and 4) avoidance of the fish to the worm. The behavior of *P. mucosa* was also noted following release from the pipette and after rejection or avoidance by the fish.

If the worm sank to the floor of the aquarium, either after rejection or without any contact with the fish, it was taken off the bottom and again dropped in front of the fish. This process was repeated as often as a 1-min trial would allow. Discounting delays due to behavioral interactions, this averaged one exposure every 6 s. Prior to the start of the first set of each test session and 1 min after each trial ended, the fish was fed a small portion of frozen brine shrimp to ensure active feeding. If at any time during a test the fish refused to eat the brine shrimp, the experiment was terminated. Because of terminations, the number of sessions per species of fish varied. Initial qualitative tests subjecting various other test organisms found on Henlopen Flats to potential predation are also noted on Table 1.

To test whether the mucoid secretion truly acts as the predatory inhibitor in *P. mucosa*, two further tests were carried out. First, mucus was removed from the surface of *P. mucosa* by repeatedly sucking the worm in and out of a narrow-mouthed glass pipette and then gently dabbing it with a clean, lintless cloth. The worm was then fed to a rock gunnel. Second, mucus from *P. mucosa* was collected by placing several of the worms in a small, dry stendor dish, allowing the worms to physically irritate each other and thus produce a copious supply of mucus. After the phyllodocids were removed from the dish, a small *Nephtys incisa*, which secretes very little external mucus, was placed in it and allowed to accumulate a thick mucoid coat. The nephtyd was then fed to the rock gunnel.

For histological study of the mucus-producing organs of *P. mucosa*, entire worms were fixed in Zenker's or Hollande's fixatives and embedded in polyester wax. Blocks were cut at 5 μm and sections stained with Mallory's "Azan" or toluidine blue in 1.0% borax.

To examine the ultrastructure of the parapodial cirri of *P. mucosa*, small worms were fixed for 1 h in cold Anderson's fixative, cut into 2 mm sections with a razor blade, thoroughly rinsed with phosphate buffer (pH 7.2), and postfixed for 1 h in 2.0% osmium tetroxide in a phosphate buffer. Following dehydration in a graded acetone series, the specimens were embedded in Spurr's low viscosity medium and polymerized at 60° C for 48 h. Thin sections, cut on a Porter-Blum[3] MT1 ultramicrotome using glass knives, were stained with uranyl acetate and Sato lead citrate. Sections were examined with a Philips EM201 transmission electron microscope at an accelerating voltage of 80 kV.

RESULTS

Response of Fish

Results of the feeding experiments for the various species of fish being fed *P. mucosa* along with the length of each are summarized in Tables 2 and

[3]Reference to trade names does not imply endorsement by the University of Delaware, College of Marine Studies or by the National Marine Fisheries Service, NOAA.

TABLE 2.—Number of attempts to ingest *Phyllodoce mucosa* by several species of fish. An attempt is defined as a single intake and expulsion of the worm. The number following the abbreviated fish binomial stands for an individual fish and the small letter that follows stands for an individual worm. The two numbers in parenthesis in the first column are the standard lengths of the fish and maximum length of the worm, in millimeters, respectively. Fh = *Fundulus heteroclitus*, Ga = *Gasterosteus aculeatus*, Mm = *Menidia menidia*, Cv = *Cyprinodon variegatus*, Lm = *Lophopsetta maculata*, Cr = Cynoscion regalis, † =experiment terminated, * = worm eaten.

	Set A, trial					Set B, trial					
Session	1	2	3	4	5	1	2	3	4	5	Total
Fh1a (63,22)	3	5*									8
Fh1b (63,29)	9	4*									13
Fh2c (66,18)	4	2*									6
Fh3d (52,19)	13*										13
Fh4e (61,19)	10*										10
Ga1a (18,9)	8	7	3	1	0	6	5	0	0	0	26
Ga2a (18,15)	21	4	0	2	1	20	5*				53
Ga2b (18,12)	2	4	0	2	1	20	5*				34
Ga3c (18,13)	29	5*									34
Ga3d (18,24)	0	0	0	0	0	0	1	0	0	0	1
Ga4e (18,12)	14	5	0	0	0†						19
Ga5e (18,12)	8	0	0	0	0†						8
Mm1a (44,24)	5	2	1	3	1	0	0	0	0	0	12
Mm2b (37,22)	4	3	1	1	0	1	1	0	0	0	11
Mm3c (51,17)	10	4	4	0	0†						18
Mm4d (54,14)	3	2	2*								7
Mm5e (64,18)	1*										1
Mm5f (64,23)	2*										2
Mm6g (67,13)	4*										4
Cv1a (46,24)	2	2	1	1	1	1	1	3	1	2	15
Cv1b (46,24)	1	1	1	1	2	2	3	4	1	0	16
Cv2c (46,14)	3	1	1	1	0	1	1	0	0	0	8
Cv2d (46,12)	2	3	3	1	2	2	3	3	3	2	24
Lm1a (69,29)	3	1	1	2	1	2	0	0	1	0	11
Lm1b (69,21)	6	4	3	1	3	5	5	3	0	1	31
Lm2a (91,29)	2	1	2	2	2	2	0	0	1	1	13
Lm2c (91,17)	2	5	5	1	3	3	3	0	0	0	22
Lm2d (91,21)	7	3	3	4	3	3	3	0	0	1	27
Cr1a (42,24)	1	2	1	1	0	0	1	0	0	0	6
Cr1b (42,16)	2	2	4	2	2	2	2	3	2	2	23
Cr1c (42,26)	0†										0
Cr2d (46,14)	2	6	1	6	5	4	5	6	4	5	44
Cr2e (46,22)	0†										0
Cr2f (46,17)	2	4	5	5	3	4	5	3	5	4	40

TABLE 3.—Number of investigations undertaken by four species of fish when exposed to *Phyllodoce mucosa*. This table excludes *Fundulus heteroclitus* and *Cyprinodon variegatus* because these species showed no or insignificant investigatory behavior without attempts at ingestion. Abbreviations and notations as in Table 2.

	Set A, trial					Set B, trial					
Session	1	2	3	4	5	1	2	3	4	5	Total
Ga1a (18,9)	0	0	0	0	4	0	0	4	3	3	14
Ga2a (18,15)	0	0	0	0	2	0	*				2
Ga2b (18,12)	0	0	0	0	3	2	*				5
Ga3c (18,13)	0	*									0
Ga3d (18,24)	3	0	2	1	1	0	0	1	0	1	9
Ga4e (18,12)	0	0	5	1	†						6
Ga5e (18,12)	0	2	2	1	†						5
Mm1a (44,24)	0	0	0	2	0	2	0	1	0	1	6
Mm2b (37,22)	4	0	0	1	0	0	0	0	0	0	5
Mm3c (51,14)	0	1	3	1	†						5
Mm4d (54,14)	0	0	*								0
Mm5e (64,18)	*										0
Mm5f (64,23)	*										0
Mm6g (67,13)	*										0
Lm1a (69,29)	0	0	0	0	0	0	0	0	0	1	1
Lm1b (69,21)	0	2	0	3	3	2	2	1	2	3	18
Lm2a (91,29)	0	0	0	0	2	0	0	0	1	0	3
Lm2c (91,17)	0	0	0	0	0	0	0	0	0	0	0
Lm2d (91,21)	0	0	0	3	2	1	2	2	0	2	12
Cr1a (42,24)	3	0	1	6	2	3	4	0	3	1	23
Cr1b (42,16)	2	1	1	3	1	3	2	4	2	4	23
Cr1c (42,26)	†										0
Cr2d (46,14)	2	0	3	2	3	2	3	1	4	3	23
Cr2e (46,22)	†										0
Cr2f (46,17)	1	2	2	2	2	1	1	3	1	4	19

TABLE 4.—Number of attempts to ingest the control polychaete *Scoloplos fragilis* and size of fish and worm used. Abbreviations and notations as in Table 2.

	Trial			Trial	
Session	1	2	Session	1	2
Fh1x (48,15)	1		Lm1w (69,16)	4	
Fh1y (48,20)	1		Lm1x(69,25)	1	
Ga1x (18,11)	1		Lm2y (91,17)	12	9
Ga2y (18, 9)	1		Lm2z (91,23)	11†	
Mm1x (37,14)	1		Cr1x (42,14)	1	
Mm2y (64,13)	1		Cr1y (42,17)	5	
Cv1x (46,13)	1				
Cv2y (46,26)	1				

3. The large number of ingestive attempts in a given trial (Table 2) resulted from the rapid, repetitive actions of a fish not allowing the worm to settle to the floor of the aquarium following initial attempts. Results of the control series using *S. fragilis* and sizes of fish and worms are given in Table 4.

Of the six species of fish quantitatively tested, only the mummichog, *Fundulus heteroclitus*, consistently ingested *P. mucosa* early in set A (Table 2). This species of fish showed no investigative behavior before taking the worm into its mouth. Nevertheless, *F. heteroclitus* did show some distaste for this polychaete; in two cases the mummichog sucked the worm in and out 13 times prior to ingestion. When *F. heteroclitus* did eat the worm, ingestion was immediately followed by a variable period (10-45 s) of choking or "coughing" (rapid protraction and retraction of jaws and intake and expulsion of water). In session Fh1a, the worm was held in the mouth and only partially ejected many times prior to ingestion. During trial 2 of set A in session Fh1b, the fish, on the fourth attempt, took in the worm and exhibited a choking response which lasted 15 s before spitting out the posterior portion of the worm. The remaining portion of the polychaete was eaten after two further attempts. The maximal number of attempts prior to ingestion by *F. heteroclitus* was demonstrated by the smallest mummichog (Fh3d) and in trials involving the largest phyllodocid (Fh1b) (Table 2). *Scoloplos fragilis* was consumed on the first attempt by *F. heteroclitus* in each control test (Table 4).

While only one size class of *Gasterosteus aculeatus* was used, there was no trend between size of the worm and ingestion by the fish (Table 2). The largest as well as some of the smaller worms were not consumed. Sessions Ga1a, 2b, and 3a all resulted in ultimate ingestion of *P. mucosa* but involved 34-53 prior ingestive attempts. Of the seven sessions observed with *G. aculeatus*, these three sessions showed the highest number of attempted ingestions prior to consumption. In session Ga2a, there was a renewed expression of the antipredation mechanism at the start of set B (Table 2). Thus, sets A and B start with 21 and 20 attempts, respectively, followed by a decrease in the number of attempts in set A and consumption in trial 2 of set B.

In most of the sessions between *G. aculeatus* and *P. mucosa*, lack of ingestive attempts seemed to correspond with the presence of investigative responses (Tables 2, 3). These investigations involved a close approach to the worm as it sank through the water column, and in some cases a recoil from the worm without evidence of direct contact. In cases where the worm was consumed, the fish exhibited a coughing response which lasted several seconds. *Gasterosteus aculeatus* readily consumed *S. fragilis* (Table 4).

A correlation between the size of the Atlantic silverside, *Menidia menidia*, and its ability to consume *P. mucosa* is suggested (Table 2). Smaller fish showed little interest in the worms following initial experiences in set A, while the larger fish often consumed the worm very early in the first set. During set A, fish <50 mm initiated several attacks on the phyllodocids, and the worm was easily taken into the buccal cavity before rejection. A rejected worm was often so densely covered with mucus that it would cling to the lower lip of the fish by a mucus thread for several seconds. *Menidia menidia* also exhibited coughing reactions following attempted and successful ingestions. Larger silversides were quick to respond to potential food items released into the aquarium and swiftly sucked them in. In set Mm5f, a 64 mm fish was fed a 23 mm worm. On the first attempt at ingestion by the fish, the worm was quickly taken, whereupon the fish reacted with a coughing response lasting 45 s. The fish also exhibited a violent lateral head shaking during this time. Following this, the worm was totally ejected but the fish continued reacting as described for several seconds. This was the only case where an entire worm was injured prior to ejection. The worm, though alive, lost several parapodia and cirri and appeared sluggish. This same worm was again placed in the aquarium with the fish and was again set upon, producing a coughing response lasting 30 s but was not rejected. This fish did postfeed on *A. marina* and *M. menidia* showed no hesitation in consuming *S. fragilis*.

Only a single size class of sheepshead minnow, *Cyprinodon variegatus*, was available. This species was exposed to *P. mucosa* ranging in size from 12 to 24 mm and showed a consistent rejection of each size class (Table 2). In no case was a coughing reaction noted. *Cyprinodon variegatus* appeared able to distinguish between *P. mucosa* and *A. marina* from short distances (up to 15 cm). The fish showed almost no investigatory behavior after initial ingestive attempts in a given trial but did quickly swim over to feed on *A. marina* in every case of exposure. *Scoloplos fragilis* was eaten on the first attempt in each control test with *C. variegatus* (Table 4).

The windowpane flounder, *Lophopsetta maculata*, was the largest fish used in this study. This species rejected the phyllodocids without fail, showing 11-31 attempts at ingestion (Table 2) and also exhibited coughing responses following ingestive attempts. The two sessions with *L. maculata*, making the greatest number of attempts to ingest (Lm1b and 2d) (Table 2), also registered the greatest degree of inquisitiveness (Table 3). There was no relation between size of fish and size of worm in these interactions. As Table 4 shows, there was some hesitation by the larger *L. maculata* in the control series when offered *S. fragilis*. In all of these control tests but one (Lm2z was terminated), the fish eventually ate the worm, but in Lm2y the fish made 21 attempts and ran into the second trial of set A prior to ingestion. Less than 1 h later, this same fish actively and quickly fed on 12 mm *Scolecolepides viridis* and 31 mm *Nereis virens*.

Juvenile weakfish, *Cynoscion regalis*, also refused to eat *P. mucosa* (Table 2). There may be a relationship between the number of attempts to ingest and the size of the worm in these cases (Table 2). In Cr1c and 2e, the worms used were among the three largest (26 and 22 mm, respectively), and in both cases the fish showed a violent headshaking response to void its buccal chamber. It thereafter became "nervous" and would not feed on *A. marina*. In Cr1a a 24 mm worm was used, and in the entire session only six attempts at ingestion were made. All the remaining *P. mucosa*

tested with *C. regalis* were <20 mm long, and ingestive attempts ranged from 23 to 44/session. *Cynoscion regalis* exhibited frequent investigative responses (Table 3) which, unlike those of most of the other fish, usually involved direct contact with the worm by bumping it with its snout. In some cases following this contact, the fish would show a headshaking reaction similar to that produced by attempted ingestion. *Cynoscion regalis* consumed *Scoloplos fragilis* during the first trials of the control series (Table 4).

During the course of these experiments, individuals of each species of fish were given the opportunity to feed on several other species of polychaetes. These included *Spio filicornis, Nephtys incisa, Nereis virens, Glycera americana, Scolecolepides viridis,* and *Hydroides dianthus*. Each fish readily consumed each of these species from several size classes, in almost every case on the first attempt.

Preliminary data has also been collected on *Eumida sanguinea* tested with *L. maculata*. Test worms ranged from 9 to 13 mm long and were consistently rejected. A 69 mm *L. maculata* rejected a 13 mm long *E. sanguinea* 20 times over a single session, while a 91 mm flounder rejected a 12 mm long worm 38 times in a session. Investigations ranged from 6 to 10/session and showed no obvious relationship with ingestive attempts. In qualitative observations, it was also noted that the rock gunnel rejected both *P. mucosa* and *P. maculata*.

Removal of the mucus coat from *P. mucosa* resulted in quick consumption by *Pholis gunnellus*. Emplacement of the phyllodocid mucus on a small *Nephyts incisa*, which were previously a quick meal for *P. gunnellus*, resulted in rejection of the nephtyd polychaete by the rock gunnel many times prior to ingestion.

Initial observations were also made on the sea robin, *Prionotus evolans*, fed *Stylochus zebra, Lineus ruber,* and *Phascoleopsis gouldi. Fundulus heteroclitus* and *C. regalis* were also tested with *P. gouldi*. In each case the fish showed adverse reactions (coughing, headshaking, and rejection) after ingestive attempts. The sea robin rejected *S. zebra* 75 times over eight trials before consuming the flatworm. In many cases, the turbellarian was held in the buccal chamber for as long as 21 s before ejection. Both the nemertean and the flatworm produced copius quantities of mucus when irritated, whereas the sipunculid did not.

Behavior of *Phyllodoce mucosa*

Phyllodoce mucosa showed relatively consistent reactions upon release into the aquarium and following rejection. When first released, the worm fell slowly through the water in a semicurl position, or curled in a tight ball and fell at a slightly faster rate. After a worm was taken and rejected by a fish, it was covered with a thick layer of viscous mucus. Immediately after rejection, the worm coiled into the tight, spheroid position. In this position, it was either retaken by the fish and the process repeated until the worm was eaten, or the worm was dropped, after initial attempts, to the floor of the tank. If the worm drifted unharmed to the floor of the aquarium, it usually started what appeared to be an exploratory phase which consisted of several short excursions in various directions before setting out on a single, straight path toward one of the corners of the aquarium. During this exploratory period, the worm held its dorsal parapodial cirri folded against its dorsum.

Histology and Ultrastructure of *Phyllodoce mucosa* Parapodial Cirri

The glandular and sensitive dorsal and ventral parapodial cirri of *P. mucosa* are the primary sources of externally released mucoid secretion.

The dorsal cirrus possesses a large nerve which runs along the cirral axis and then radiates centrally into several smaller nerves which wind between the large cirral mucocytes (Figure 1). Numerous free neural extensions penetrate the cirral epithelium. Large, ovoid mucocytes, which stain beta-metachromatically with toluidine blue (Figure 1, lower), fill most of the cirrus. These broad and elongated cells have small basal nuclei. In worms that have been irritated prior to fixation, the previously metachromatic mucocytes appear as large, empty vacuoles surrounded by many immature mucus cells (Figure 1, upper). The latter are usually small, irregularly shaped cells which are densely packed with basophilic but orthochromatic secretory granules. The outer, central portion of the dorsal cirrus has a narrow bank of melanic pigment cells. There are also thin muscle bands which enter the cirrus along the dorsal region of the cirral peduncle.

Electron microscopy reveals a dense microvillar and ciliary border lining the short, columnar epithelium of the dorsal cirrus (Figure 2). The epithelial cells have large, irregular nuclei with

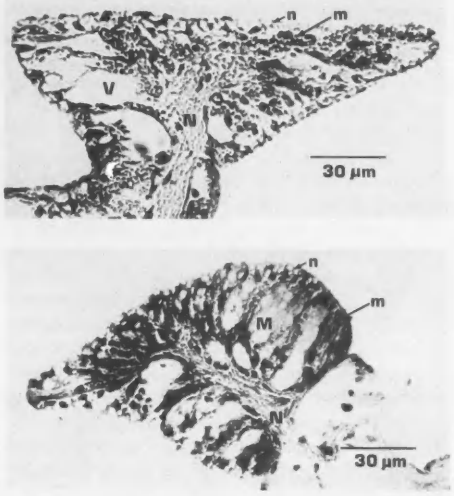

FIGURE 1.—Upper: An oblique-frontal section of the dorsal parapodial cirrus of the polychaete *Phyllodoce mucosa*. This specimen was irritated prior to fixation resulting in the loss of the mucoid secretion produced by mature cirral mucocytes. The vacuolated regions mark the remnants of the mature mucocytes. The large cirral nerve is also evident. Zenker's fixative, "Azan" stain. m = immature mucocyte; n = neural extension; N = cirral nerve; V = vacuolated mucocyte. Lower: The dorsal parapodial cirrus of a relaxed specimen of *P. mucosa* in transverse section, fixed without excessive mucus loss. The cirral mucocytes show a beta-metachromatic reaction with toluidine blue. Hollande's fixative, toluidine blue stain. M = metachromatic mucocyte.

abundant heterochromatin material. Many immature secretory inclusions are present near the epithelial surface as well as subepithelially. The immature secretory droplets occur in a loose formation and are surrounded by a dense array of smooth endoplasmic reticulum. The larger, less electron dense, mature secretory droplets occur in tighter, membrane bound accumulations. Figure 2 shows a portion of a vacuolated mucous cell bounding a central nucleus. Both the mature and vacuolated secretory cells have numerous, small mitochondria associated with them.

The smaller, ventral cirrus is histologically and cytologically similar to the dorsal cirrus, and is equipped with oblong mucocytes in both mature and immature stages. Also present is a large cirral nerve and thin longitudinal muscle bands. Melanic pigmentation is not obvious in sections of the ventral cirri.

DISCUSSION AND CONCLUSIONS

Many factors influence successful predation. Griffiths (1975) believed that prey abundance and prey size are two of the prime variables affecting predation success but that situations do occur in which predators react to prey characteristics other than body size. These characteristics include physical avoidance by potential prey (Fagade and Olaniyan 1973) which may be chemically mediated by a secretion released by the predator (Mackie et al. 1968; Doering 1976; Mayo and Mackie 1976), physical deterrents of the potential prey species such as spines (Hoogland et al. 1956; Bakus 1966), or innate defense mechanisms of the potential prey such as toxicity or unpalatability (Thompson 1960; Bakus 1966, 1968; Gibson 1972; Rahemtulla and Løvtrup 1974). An epidermal, mucoid secretion is responsible for the protection of at least some phyllodocid polychaetes from active predation by some small or juvenile fish. Since phyllodocids are relatively small benthic worms, it is unlikely that many large fish would expend the energy needed to use them as a primary food source; thus only smaller fish would potentially make any notable impact on the phyllodocid populations.

Russell (1966) tested the palatability of tissues from 48 species of marine organisms with two marine (*Pelatus quadrilineatus* and *Torquigener hamiltoni*) and two freshwater (*Gambusia affinis* and *Carassius auratus*) species of fish ranging from 25 to 90 mm. This involved choice experiments with the fish simultaneously offered a known palatable organism and a test organism of unknown palatability. The results revealed many unpalatable species which were rejected by the fish. The majority of these tests involved only three or fewer trials and there is little note concerning specific reaction of fish to potential prey items. Among the palatable items found by Russell was *Phyllodoce malgremi*. Phyllodocids, as all other test organisms, were cut to acceptable sizes based on preliminary trials which noted size limits of prey for each fish. *Phyllodoce malgremi* might indeed be consumed by these particular fish but the limited number of trials (two per fish) and lack of corresponding worm size data plus the previous treatment of the worms (i.e., sectioned into fragments) may have led to misleading data concerning palatability.

Few reports list phyllodocids as a major portion of a fish's diet; however, Wigley (1956) did list four

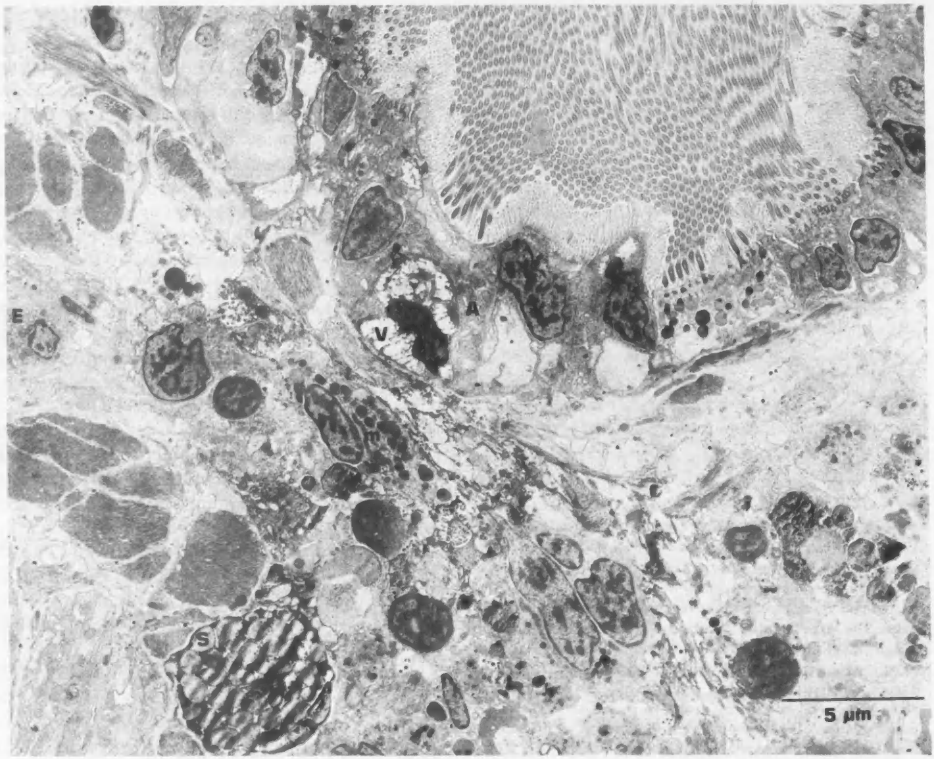

FIGURE 2.—The ultrastructure of the dorsal parapodial cirrus of the polychaete *Phyllodoce mucosa*. The micrograph shows the dense array of cilia and microvilli which line the cirral epithelium as well as mature and immature secretory droplets and associated organelles. Anderson's and osmium tetroxide fixation, uranyl acetate, and Sato lead stain. S = mature secretory droplets; A = mitochondria; E = smooth endoplasmic reticulum. Other abbreviations as in Figure 1.

species of phyllodocids in the food of the haddock, *Melanogrammus aeglefinis*. No phyllodocids were among the 11 dominant prey species of the larger fish examined. Wigley noted, however, that because of the small, subterminal mouth, most of the haddocks' prey were small and thin. Small invertebrates, including phyllodocids, were listed as dominant foods of the few smaller (14-30 cm) haddock examined. Annelids composed only 1.9% of the prey items found in the haddock study and no note was made of the diet of fish <14 cm. Data for small juveniles is found in only a few studies involving bulk analysis of fish stomach contents (Stickney et al. 1975; Chao and Musick 1977).

In nature, initial rejection and adverse reaction of a fish to *P. mucosa* may give the potential prey sufficient time to retreat from harm. Chiszar and Windell (1973) found that satiated bluegill, *Lepomis macrochirus*, have more selective feeding habits than starved fish. This may imply that in natural conditions a normally feeding fish may not persist in an attack on an unpalatable prey organism.

Murdoch et al. (1975) suggested that predators distribute attacks among prey species in response to the prey's relative densities. These authors broke down events leading to final ingestion of prey into a series of predatory behaviors, including "choosing" to attack the prey species. Once a potential prey is perceived and located, the "choice" is up to the predator whether to attack or not. If the organism is attacked and successfully

consumed, the predator may set up a "specific searching image" (Tinbergen 1960), which would increase its chance of locating additional specimens provided more of the same prey species can be found while reinforcement is still fresh. Thus, this pattern is only relevant when prey species occur in relatively high densities. *Phyllodoce mucosa* is found in moderately high densities in Nahant Bay with many other polychaetes such as *Prionospio malmgreni, Scoloplos armiger,* and *Nephtys* spp. If a small fish encounters and attempts to eat a *Phyllodoce mucosa* but is repulsed by the worm's defenses several times, the fish may eventually set up a negative searching image and thus avoid further "discomfort" caused by attempted ingestion. While simultaneous choices of food may be a rare event in nature (Beukema 1968), when it does occur between a phyllodocid and another type of prey of similar size, a fish with a negative image may "select" the nonphyllodocid prey. This is indicated in the present data by the relationship between ingestive attempts and investigations of *Gasterosteus aculeatus* and the "loss of interest" shown by the smaller *Menidia menidia*.

Kneib and Stiven (1978) recently found that the diet of *F. heteroclitus* in a North Carolina salt marsh varied with the size of the fish (smaller fish were carnivorous while larger individuals were omnivorous). In this case, alteration in diet seemed to reflect a physiological and morphological change in the fish with growth. This conversion of food habits may be based upon the ability of the fish to eat different food items because of its proportionally larger size or it might indicate a change in the "ability" of the fish to consume less appealing food items if the "need" arises. Data presented here indicate that larger *M. menidia* might be more effective in consuming phyllodocids than smaller *M. menidia*. Smaller fish may not be able to "handle" a phyllodocid of a size that a larger fish might readily consume. This is based solely upon the reaction of the fish to the mucoid secretion since smaller fish were able to consume comparatively large nonphyllodocid polychaetes.

The largest fish used in the present study, a juvenile *Lophopsetta maculata*, about 9 cm long, consistently rejected *P. mucosa*. *Lophopsetta maculata* is an active predator of mobile prey (Table 1). The large buccal chamber and distensibility of the esophagus of this flounder preclude the possibility that the phyllodocid mucus acts as a physical barrier to ingestion (i.e., an occlusive plug) but instead indicate that the mucus contains some irritating or obnoxious substance which repels the fish.

The high sensitivity and secretory nature of the parapodial cirri is reflected in the complex ultrastructure shown in Figure 2, however, *P. mucosa* does not seem able to continually produce an adequate supply of protective mucus. This is indicated by ingestion of the worm by *G. aculeatus* following numerous rejections from this fish's small, sharply toothed buccal cavity which may have removed the protective cover. Similar results are obtainable with a smallmouthed pipette, which simulates this. The large, empty vacuoles in the dorsal cirri surrounded by immature mucocytes indicate a lag between total loss of available secretion and maturation of additional, functional mucocytes.

Beukema (1968) suggested that *G. aculeatus* hunts by sight only and its sense of smell plays little if any role in finding food. This is supported in the data presented here by the correlation between investigations and ingestive attempts. Investigations involved no direct contact but only close observation of the worm by the fish.

Ejectory behavior by *G. aculeatus* feeding on clumps of *Tubifex* spp. oligochaetes was discussed by Tugendhat (1960) who found that this action caused a breakdown of the clumps into individual worms which were easily ingested. Hynes (1950) noted that young *G. aculeatus* feed on proportionally smaller prey items and that the diet changed to larger prey as the fish grew. The largest phyllodocid fed to a *G. aculeatus* in the present study was 24 mm long, and it was investigated but only one attempt at ingestion was made. In this case, the worm probably was too large for the fish to deal with.

The only species of fish tested which consistently ate *P. mucosa* was *F. heteroclitus*. *Fundulus heteroclitus*, a well-known inhabitant of salt marshes, is only rarely found in strictly saline environments (Hildebrand and Schroeder 1928). Vince et al. (1976) showed that *F. heteroclitus* may cause an impact on the abundance and distribution of some prey species, and Fraser (1973) found that *Fundulus* spp. would consume prey items in proportion to prey densities. Since *P. mucosa* is not a normal resident of salt marshes the question must be asked: does the fact that these two organisms occur in different environments influence the predator-prey interactions between these species when brought together? According to Tin-

bergen (1960), there may be an obvious delay in the attack on a potential prey if it is new to the predator. No such delay was seen in these experiments using semistarved fish. It is unlikely that *P. mucosa* has developed a defense mechanism which is specific in its action only to marine fish. The ability of *F. heteroclitus* to consistently consume *P. mucosa* probably reflects the predaceous mummichog's lack of sensitivity or its ability to overcome the irritation or unpalatability of this worm.

Cyprinodon variegatus always rejected the phyllodocids and rarely investigated the worm without attempted ingestion. The small, terminal mouth of this fish, with its large tricuspid teeth and protractile premaxillaries, was quite efficient at quickly devouring all nonphyllodocid polychaetes offered to the fish during these experiments.

Cynoscion regalis is primarily an active pelagic predator (Table 1). There has been some research concerning the feeding habits of juvenile sciaenids (Thomas 1977; Chao and Musick 1977) which found that small *C. regalis* feed mainly on mysids, copepods, and small fish. Annelids do form, however, a portion of the weakfish's diet (Table 1). Bigelow and Schroeder (1953) noted that the diet of *C. regalis* varies with locality and availability of prey. Small weakfish reject *P. mucosa* as a food item. *Cynoscion regalis* showed active investigatory behavior which usually consisted of tapping or bumping the sinking worm with its snout. Direct contact often resulted in a rapid shunning of the worm by the fish. This may indicate the presence of sensitive nares chemoreceptors. The juvenile fish would not be a major threat to these worms even were they readily available.

Preliminary work indicates that antipredation responses are active in *P. maculata, E. sanguinea, Phascoleopsis gouldi, Stylochus zebra,* and *Lineus ruber*. All these organisms, except the sipunculid, secrete large quantities of mucus. The epidermis of many sipunculids is densely packed with gland cells (Tétry 1959) and some secretion from these glands may serve to protect the animal from predation. *Stylochus zebra*, is a commensal of pagurid crabs; abundant production of mucus by this worm may tend to keep this relationship commensal.

The role of secretory defense mechanisms is well established in many species of marine animals (Graham 1957; Thompson 1960, 1969; Bakus 1968), but many questions concerning the broader aspects of antipredational responses remain unanswered. Are antipredation responses reflected in the composition of marine benthic communities? How does effectiveness of antipredation mechanisms vary with size of predators or degree of predator satiation? In similar-sized predators, what differences allow one species to prey on a given organism and not on the other? What changes in diet would be found if feeding studies involving analyses of stomach contents typically were extended to include all size classes of fish? Does previous exposure to an antipredation mechanism produce "learning" in potential marine predators?

In responding to slow-moving predators many potential prey species have evolved escape reactions (Doering 1976). In dealing with highly mobile fish predators, many species of potential prey have developed such defense mechanisms as protective secretions. Lagler et al. (1977:142) stated, "In general the esophagus [of fish] is so distensible that it can accommodate anything that the fish can get into its mouth . . . ." With the discovery of the repulsive characteristics of certain phyllodocids, the indications of antipredation mechanisms in a sipunculid and turbellarian reported here, added to what is known of nemerteans and opisthobranchs, it is clear that a closer examination must be made of interspecific molecular interactions which occur within marine communities.

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CONTRIBUTION OF WILD AND HATCHERY-REARED COHO SALMON, *ONCORHYNCHUS KISUTCH*, TO THE OREGON OCEAN SPORT FISHERY

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ABSTRACT

Eight scale characters of known hatchery and wild coho salmon, *Oncorhynchus kisutch*, were compared, and a linear discriminant function was used to determine whether hatchery and wild adult coho salmon could be reliably separated on the basis of scale characteristics. Attempted separation was based upon known differences in rearing environments of hatchery and wild juvenile coho salmon and upon hatchery smolts being larger than wild smolts. Identifications were correct for 82% of the hatchery fish and 89% of the wild fish. Based on analysis of scales from adult coho salmon of unknown origin (hatchery or wild) and the estimated catch of marked, hatchery-reared coho salmon taken by the Oregon sport fishery, we concluded that 75% of the fish caught in the ocean along the Oregon coast from mid-June to mid-September 1977 had been released as smolts from hatcheries. Percentages of hatchery fish in the catch ranged from 85 near the mouth of the Columbia River to 61 at Winchester Bay on the central Oregon coast. Fisheries along the south and central Oregon coast may have had access to higher percentages of wild coho salmon after mid-August than prior to this time, probably because wild fish from coastal streams remained near these ports, whereas most fish destined for Columbia River hatcheries had already migrated northward.

The coho salmon, *Oncorhynchus kisutch*, is the most abundant species of salmon contributing to Oregon's commercial troll and ocean recreational fisheries (Oregon Department of Fish and Wildlife[3]). Numbers of this species caught commercially in Oregon have historically fluctuated widely. Catches from 1952 to 1962 averaged 292,000 fish and ranged from 551,000 in 1957 to 112,000 in 1960. Numbers of coho salmon caught increased generally in 1963-77 and averaged 860,000 fish/yr while ranging from 1,827,000 in 1976 to 450,000 in 1977. Catches by the Washington and California troll fisheries have also increased in recent years (Wright 1976; Pacific Fishery Management Council 1978). This rise in catch has been attributed to increased production by Federal and state hatcheries of larger and healthier smolts (Pacific Fishery Management Council 1978; Reed[4]).

This increased abundance of coho salmon has coincided with, and partly led to, the development of a substantial sport fishery in the ocean off Oregon, Washington, and California. The number of coho salmon caught in the ocean by sport fishermen has been fairly stable in Oregon since 1964 but has increased rapidly in Washington since the early 1960's (Phinney and Miller 1977; Pacific Fishery Management Council 1978).

Although both total releases of coho salmon smolts from public hatcheries and catch have increased, indices of escapement of wild fish indicate that the numbers of wild coho salmon spawning have decreased (Cummings[5]). In an analysis of counts of spawning salmon from selected areas of eight Oregon coastal streams from 1964 to 1974, we found that counts of adult salmon have declined significantly in the Nestucca ($P<0.01$), Alsea ($P<0.01$), Yaquina ($P<0.05$), and Coquille ($P<0.005$) Rivers and Beaver Creek ($P<0.05$), but no significant trends were observed in the Nehalem, Wilson, and Coos Rivers. For all spawning areas combined, the conclusion is that overall escapements are declining ($P<0.01$) on coastal

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[3]Oregon Department of Fish and Wildlife. 1977 unpubl. stat. of troll salmon investigations group. Marine Science Drive, Bldg. #3, Newport, OR 97365.

[4]Reed, P. H. 1976. A history and current status of Oregon ocean salmon fisheries-troll salmon investigations. Oregon Department of Fish and Wildlife, Marine Science Drive, Bldg. #3, Newport, OR 97365.

[5]Cummings, E. 1977. Spawning coho and chinook salmon surveys in coastal watersheds of Oregon. 1976. Oregon Department of Fish and Wildlife, 17330 SE Evelyn Street, Clackamas, OR 97015.

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rivers (Berry[6]; Cummings see footnote 5). The escapement of wild fish is also declining in the lower Columbia River (Oregon Department of Fish and Wildlife and Washington Department of Fisheries 1976).

Management agencies do not know how many wild fish are caught in Oregon's troll and sport fisheries, even though they strongly suspect that the number of wild fish in the catch is smaller now than it was 10 yr ago. If they knew the numbers of hatchery and wild fish contributing to Oregon's fisheries, they could recommend management strategies according to the needs of the respective stocks. Also, if they could distinguish hatchery and wild fish caught in the fisheries at various times and localities, they could determine the potential for differentially harvesting the stocks. Consequently, we elected to attempt separating hatchery and wild coho salmon caught in the Oregon ocean sport fishery by measuring and counting characters of scales taken from adult fish. Our objective was to determine the percentages of hatchery and wild fish contributing to the Oregon ocean sport fishery at different times and locations.

METHODS

Scales are a logical choice for separating hatchery and wild coho salmon, since they have been used to differentiate stocks of salmon in rivers (Henry 1961), and for classifying mixed stocks of salmon caught on the high seas to continent of origin (Mosher 1963; Tanaka et al. 1969; Anas and Murai 1969). A review of the use of scales for identification of stocks of salmon was given in Major et al. (1972). Peck (1970) successfully differentiated between hatchery and wild juvenile coho salmon by using several scale characters.

Scales from coho salmon of known hatchery origin (identified by missing adipose fins), and scales of unmarked salmon of unknown origin were collected by personnel of the Oregon Department of Fish and Wildlife from adult fish captured in the ocean by sport fishermen from mid-June to mid-September 1977. Samples were collected weekly from eight coastal ports, listed from north to south: Hammond, Garibaldi, Depoe Bay, Newport, Winchester Bay, Coos Bay, Gold Beach, and Brookings. We obtained scales from 178 adipose clipped salmon and from 2,054 unmarked salmon (Table 1).

Because few wild fish were available, we had to use wild fish of several different brood years to increase our sample. Geographic location, brood year, and number of scale samples used in the subsequent analysis are shown in Table 2.

Two nonregenerated scales obtained from the left side of each fish, one to four rows above the lateral line between the dorsal and adipose fins, were mounted on gummed cards, and acetate impressions were made by methods similar to those described by Clutter and Whitesel (1956). A conscious effort was made to select the largest nonregenerated scales within each sample. Scale impressions were read with the aid of a projector at a magnification of 80×.

Based on Peck's (1970) analysis of scale characters of hatchery and wild smolts of coho salmon and on our analysis and observations of scale characters from known wild adult fish and those from three Oregon hatcheries, we selected eight characters that we believed were potentially useful in separating hatchery from wild fish (Table 3). Characters were selected based on the assumption that the freshwater rearing environments for hatchery and wild coho salmon are distinctly different and differences in scales between the two groups would be manifest during this period.

We selected for analysis preocean radius and preocean circulus counts on the basis of results of Peck (1970) and on data on weights of smolts being

TABLE 1.—Number of adipose clipped and unmarked coho salmon sampled for scales at Oregon ports in 1977. Ports are arranged from north to south.

Port	Marked	Unmarked	Port	Marked	Unmarked
Hammond	5	356	Coos Bay	9	165
Garibaldi	43	188	Gold Beach	0	30
Depoe Bay	64	516	Brookings	0	56
Newport	33	412			
Winchester Bay	24	331	Total	178	2,054

TABLE 2.—Origin of scales of wild coho salmon, brood year, and number of scale samples from each geographic location.

River system	County of collection	Brood year	Number of samples
Necanicum	Clatsop	1974	3
Salmon	Lincoln	1973	45
Salmon	Lincoln	1974	16
Alsea (Flynn Creek)	Lincoln	1962	7
Alsea (Flynn Creek)	Lincoln	1963	32
Alsea (Needle Branch)	Lincoln	1963	27
Alsea (Deer Creek)	Lincoln	1963	28
Coos and Coquille	Coos	1974	4
Total			162

[6]Berry, R. L. 1975. Spawning surveys in coastal watersheds. 1974. Oreg. Dep. Fish Wildl. Coastal Rivers Inf. Rep. 75-4. P.O. Box 529, Tillamook, OR 97141.

TABLE 3.—Description of scale characters measured or counted in this study from known hatchery and wild coho salmon. All measurements are made at angles ventral to the longest axis.

Character	Description
1	Radius of preocean zone at 20°
2	Number of circuli in the preocean zone at 20°
3	Distance between circuli 1 and 5 of the preocean zone at 90°
4	Distance between circuli 1 and 10 of the preocean zone at 90°
5	Distance between circuli 1 and 15 of the preocean zone at 90°
6	Radius of preocean zone at 90°
7	Number of circuli in preocean zone at 90°
8	Number of broken or branched circuli within precisely defined zone (see Methods).

released by hatcheries of the Oregon Department of Fish and Wildlife. Most hatchery-reared smolts currently being released by Oregon's hatcheries are larger than wild smolts (Oregon Department of Fish and Wildlife[7]). Because radii of scales and number of circuli appear to be well correlated to length of Pacific salmon smolts (Clutter and Whitesel 1956), they are logical selections for scale characters to use in separating hatchery and wild fish.

Some scales had no "plus" (Anas and Murai 1969) or estuarine growth whereas others had substantial amounts. We chose to measure total freshwater growth plus any spring and estuarine growth and to call that distance the "preocean" zone.

We chose three spacing characters, 3 through 5 (Table 3), to determine whether the plentiful food supply of hatchery coho salmon would yield different spacing of circuli than that observed for wild fish. We measured these characters at 90° to the longest axis of the scale because breaking and branching of circuli is less at that angle than at lower angles to the longest axis.

The number of broken or branched circuli (character 8, Table 3) was used to determine if circuli of hatchery fish were more or less branched than circuli of wild fish. It was postulated that regular feeding by hatchery fish would result in less breaking and branching of circuli. For this character an acetate sheet with thin parallel lines 1 cm apart and a dotted line parallel to and midway between these lines was used as a guide. A small point at the end of the dotted line was placed at the center of the focus of the scale and a dotted line extended outward at 90° ventral to the longest axis. The two solid outer lines then enclosed a rectangular area. Within this area, we counted circuli 5 through 12 inclusive in the preocean zone of the scale and recorded the number of these circuli that were broken or branched.

The eight characters in Table 3 were measured and counted from scales of known hatchery fish (Table 1) and known wild fish (Table 2). These measurements were subjected to discriminant function analysis, which reduced all characters for each scale to a single value and then, through a linear model, classified the scales as hatchery or wild (Nie et al. 1975). Assumptions in this analysis were that data were multivariate normal and had common variance-covariance matrices. Plotting the data for each of the eight characters individually showed that only character 8 deviated somewhat from normal. Although normality of individual characters does not imply joint normality, it indicates that the data conform fairly well with the assumption of multivariate normality.

From the discriminant function analyses, it was concluded that preocean radius at 20° (character 1) was the most efficient individual character for separating hatchery and wild fish. Preocean radius at 20° is generally larger in hatchery fish than in wild fish. By using the character, we reliably separated 82% of the hatchery fish and 89% of the wild fish.

While characters 1, 3, and 8 in combination would do as well, there would be no benefit to their use except that a slightly higher percentage (1.1) of hatchery fish would be correctly classified at the expense of a lower percentage (1.2) of wild fish correctly classified (Table 4).

Since preocean radius at 20° was the most useful character for discriminating between adult hatchery and wild coho salmon, this character was mea-

TABLE 4.—Combinations of scale characters to which discriminant function analysis was applied and effectiveness at classifying coho salmon as to wild or hatchery origin.

Character	Percentage correctly classified		
	Hatchery	Wild	Total
1	81.5	88.9	85.0
2	69.7	82.1	75.6
3	74.7	72.8	73.8
4	69.1	81.5	75.0
5	75.3	75.3	75.3
6	78.7	85.8	82.1
7	70.2	69.1	69.7
8	68.0	65.4	66.8
1, 8, and 3	82.6	87.7	85.0
1 and 2	79.8	88.9	84.1
1 through 8	82.6	87.0	84.7
1, 8, 3, 2, and 5	81.5	87.0	84.1

[7]Oregon Department of Fish and Wildlife. Unpubl. stat. of the Fish Culture Division. 17330 SE Evelyn Street, Clackamas, OR 97015.

sured from scales from 2,054 unmarked coho salmon (Table 1). In all scale readings only scales that had one or more ocean annuli were read. Fewer than 0.5% of the fish were age 2.1, and the scales indicated that the fish grew slowly in their first year of life.[8] These scales were assumed to be from wild fish.

Wild and hatchery fish were assumed to have similar numbers of regenerated scales, most of which were regrown because of scale loss during freshwater rearing. If wild fish tend to lose more scales because of their more rigorous rearing environment in freshwater, the numbers of wild fish are slightly underestimated, since those samples taken from unmarked salmon that were discarded for lack of useable scales would have been biased toward being wild fish.

Once we had classified scales from unmarked fish as hatchery or wild we weighted the number of unmarked fish that were landed at each port during 2-wk periods (sampling strata) for the season by our estimated percentages of hatchery and wild fish for that stratum. The estimated catch of known marked fish was then added to the unmarked hatchery fish to find the total number of hatchery fish caught in that stratum (Table 5).

Because of the small number of scales available from unmarked fish for several strata, we combined 2-wk periods for a given port where necessary to obtain a sample of at least 50 fish. Small sample sizes necessitated combining samples for Brookings and Gold Beach.

The observed percentage of hatchery coho salmon in the unmarked sample was corrected for wild fish incorrectly classified as hatchery fish, and hatchery fish incorrectly classified as wild fish. Confidence levels were also computed. Both procedures are described by Worlund and Fredin (1962).

RESULTS

The percentages of hatchery fish contributing to Oregon's sport fishery were highest near the Columbia River and decreased steadily southward (Table 6). The percentages of wild fish in the catch were highest late in the season at Garibaldi, Depoe Bay, Newport, and Winchester Bay and near midseason at Hammond. Total estimated percentages of hatchery fish landed at each port from mid-June to mid-September 1977 were 85 at Hammond, 83 at Garibaldi, 79 at Depoe Bay, 77 at Newport, 61 at Winchester Bay, 65 at Coos Bay,

[8]Most adult coho salmon caught off Oregon are age 1.1, where numbers left and right of the decimal indicate number of freshwater and marine annuli on the scales, respectively. Age 1.1 fish are in their third year of life.

TABLE 5.—Estimated number of coho salmon landed and the catch per angler day (in parentheses) by Oregon sport fishery by port in 1977. Data are for 2-wk periods from 16 June to 15 September.

Port	16-30 June	1-15 July	16-31 July	1-15 Aug.	16-31 Aug.	1-15 Sept.
Hammond	5,548	10,058	12,701	11,810	5,056	1,845
	(1.34)	(1.33)	(1.35)	(0.88)	(0.45)	(0.36)
Garibaldi	217	859	2,285	1,438	1,625	279
	(0.06)	(0.28)	(0.45)	(0.24)	(0.28)	(0.09)
Depoe Bay	1,090	2,624	7,909	2,927	5,032	616
	(0.24)	(0.32)	(0.70)	(0.28)	(0.46)	(0.13)
Newport	568	2,447	4,349	4,492	3,283	516
	(0.11)	(0.27)	(0.41)	(0.59)	(0.43)	(0.16)
Winchester Bay	2,602	5,328	10,175	9,217	1,639	1,287
	(0.65)	(0.57)	(0.99)	(0.65)	(0.24)	(0.27)
Coos Bay	641	1,923	3,522	1,553	638	244
	(0.23)	(0.33)	(0.60)	(0.35)	(0.13)	(0.14)
Gold Beach	9	2	812	337	68	17
	(0.05)	(0.00)	(0.29)	(0.08)	(0.02)	(0.01)
Brookings	33	19	8,603	2,141	96	180
	(0.01)	(0.00)	(0.49)	(0.16)	(0.03)	(0.04)

TABLE 6. — Estimated percentages and 95% confidence intervals of hatchery-reared coho salmon in the total catch landed in 1977 by the Oregon sport fishery.

	Period					
Port	16-30 June	1-15 July	16-31 July	1-15 Aug.	16-31 Aug.	1-15 Sept.
Hammond	(91.8±5.6)		69.2±11.7	90.9±6.2	(90.6±5.3)	
Garibaldi	(84.8±7.3)			(80.8±8.0)		
Depoe Bay	79.7±6.7	95.7±4.4	88.3±6.4	68.6±12.0	(64.1±7.8)	
Newport	100.0±0.2	92.3±5.5	(74.1±6.1)		(72.0±10.9)	
Winchester Bay	(64.5±11.7)		70.7±7.3	(49.7±8.9)		
Coos Bay	(58.9±10.3)		(67.3±10.3)			
Gold Beach/Brookings	(62.8±10.1)					

and 63 at Brookings/Gold Beach. An estimated 75% of all coho salmon landed by the entire sport fishery from mid-June to mid-September 1977 originated from hatchery releases. Percentages of hatchery coho salmon by port and period, along with confidence intervals, are shown in Table 6.

Since the sport fishery is mainly composed of private and charter boats on day-long trips, our estimated percentages of hatchery and wild fish by port probably reflect fairly well the actual percentages occurring near each port, assuming similar catchability of hatchery and wild fish.

DISCUSSION

Of the estimated 140,660 coho salmon caught in the ocean in 1977 by Oregon sport fishermen from mid-June to mid-September, 35,300 were wild fish. Although scales from fish caught by the commercial troll fishery were not analyzed in 1977, it is likely that the overall percentages of wild and hatchery fish were similar to those of sport fishery. To evaluate this likelihood, we compared observed percentage of marked fish in the monthly catch of the sport fishery for six Oregon ports with the percentage of marked fish in the corresponding commercial catch. In only 7 of the 18 comparisons for which sample sizes were adequate did percentages of marked fish caught in a given strata by the sport fishery differ from those of the commercial fishery ($P<0.05$), which indicates that overall percentages of hatchery and wild fish are similar for the two fisheries.

We can explain the north to south trend toward increasing percentage of wild fish in the catch (Table 6) by assuming a northward movement of hatchery and wild coho salmon as the season progresses, as Van Hyning (1951) concluded, with wild fish from south and north coastal streams ceasing their northward movement near their natal streams. Since over 80% of the coho salmon produced by hatcheries in California, Oregon, and Washington (excluding Puget Sound) are released in the Columbia River and its tributaries (Oregon Department of Fish and Wildlife see footnote 7), many of the hatchery fish off the Oregon coast are probably headed for the Columbia River. These hatchery fish continue northward and concentrate near the mouth of the Columbia River. The argument for south to north movement of coho salmon is supported by the occurrence of lower percentages of hatchery fish late in the fishing season in catches off of Garibaldi, Depoe Bay, Newport, and Winchester Bay (Table 6). Late in the season, hatchery fish may be proportionately less abundant along the south and central coast, since most Columbia River fish would have moved northward by this time, leaving mostly coastal hatchery and wild fish contributing to the south and central coast fisheries. The lowest percentage of hatchery fish noted was 49.7 at Winchester Bay, from 1 August to 15 September.

Another possible factor contributing to lower percentage of hatchery coho salmon in the fishery to the south is that a substantial portion of adult hatchery fish released as smolts from Columbia River hatcheries do not migrate far southward along the Oregon coast. The argument is supported by the large number of coho salmon caught per angler day at Hammond early in the fishing season (Table 5), perhaps indicating that coho salmon returning to the Columbia River are concentrated near the river in early summer. The high percentage of hatchery fish caught at Hammond from 16 June to 15 July further supports this hypothesis (Table 6).

The total catch of coho salmon and catch per angler day were low after mid-August 1977 from Winchester Bay southward, and were low for all ports after August (Table 5), so that while the percentage of wild coho salmon caught rose late in the season, the numbers caught were low, especially along the southern coast. Closing the season for salmon fishing after mid-August would not have protected many wild coho salmon, and would have made only a small sacrifice in catch of hatchery fish. Almost twice as many chinook salmon, *O. tshawytscha*, would have been lost to the sport fishery.

Combined data obtained from the Oregon Department of Fish and Wildlife from Winchester Bay to Brookings from mid-August to mid-September showed that an estimated 1.8 chinook salmon were caught for every coho salmon landed by sport fishermen. During years of higher abundance of coho salmon, fishermen may tend to fish more for coho and less for chinook salmon than they did in 1977, which would increase fishing pressure on wild stocks of coho salmon late in the season.

If wild and hatchery fish are distributed differently in oceanic areas, fishing pressure could be adjusted to meet management goals. If, however, there is substantial variability in the localities of capture of wild fish, either because of the fishery or because of environmental factors, and if hatchery

fish intermingle extensively with wild fish, it will be difficult to protect wild stocks while maintaining high rates of harvest of hatchery fish in the ocean.

Total Oregon troll and sport catch of coho salmon in the ocean plus the Columbia River commercial catch was only 645,000 fish in 1977. Assuming that 75% are hatchery fish, only 162,000 of the fish originated from natural production. Average annual catch of coho salmon by the Oregon troll fishery alone from 1952 to 1956 was 312,000 fish, probably almost all wild fish. The lowest catch over the 5-yr period was 227,000 fish in 1954. This figure excludes fish caught in the ocean by sportsmen and also excludes the Columbia River catch. The average catch from 1952 to 1956 was 1.9 times higher than the catch of wild coho salmon from the combined ocean troll and Columbia River net fisheries in 1977. Yet, the catch of wild fish in the 1950's was considered low enough to warrant closure of commercial gill net fisheries in all Oregon coastal streams to increase the escapement of wild stocks. The efficient net fisheries of the 1950's were considered a primary threat to the production of wild salmon by some biologists. Recent analyses of marking experiments with coho salmon show some Oregon coastal stocks of hatchery fish with a catch to escapement ratio of 6 (Pacific Fishery Management Council 1978). Assuming wild fish are as readily catchable as hatchery fish, the effectiveness of the troll and offshore sport fisheries in harvesting coho salmon now rivals that of many terminal fisheries. Despite elimination of coastal Oregon net fisheries, abundance of wild coho salmon, from all indications of catch and escapement, is at an alltime low.

The catch of wild fish might be considerably less if it were not for the natural spawning of some hatchery fish and later rearing of their progeny in streams. The number of wild coho salmon that results from natural spawning of hatchery fish that fail to return to hatcheries is unknown. Considering the large numbers of smolts being released, even a small percentage of straying by returning adults could lead to significant production in the wild, assuming that the progeny do not differ significantly in fitness from the progeny of wild parents.

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LARVAL MORPHOLOGY OF *PANDALUS TRIDENS* AND A SUMMARY OF THE PRINCIPAL MORPHOLOGICAL CHARACTERISTICS OF NORTH PACIFIC PANDALID SHRIMP LARVAE

EVAN HAYNES[1]

ABSTRACT

Larval stages I-VII of *Pandalus tridens* from plankton of lower Cook Inlet, Alaska, are most similar morphologically to larvae of *P. borealis*, *P. goniurus*, *P. jordani*, and *P. stenolepis* from the North Pacific Ocean. Larvae of *P. tridens* are distinguished from larvae of *P. borealis*, *P. goniurus*, and *P. jordani* by the shape of the rostrum and antennal scale, and spination of the abdominal somites. Larvae of *P. tridens* differ from larvae of *P. stenolepis* by shape of the carapace, abdominal somites, and telson; length of the antennal flagellum and rostrum; and setation of the antennal scale. Differences in larval morphology support classification of *P. tridens* as a species rather than a subspecies of *P. montagui*. A summary of the principal morphological characteristics of the described larvae of pandalid shrimp found in the North Pacific Ocean is provided.

In 1976, the Northwest and Alaska Fisheries Center Auke Bay Laboratory of the National Marine Fisheries Service and the Alaska Department of Fish and Game conducted a survey to determine the seasonal distribution of larvae of king crab and pandalid shrimp in the Kachemak Bay-lower Cook Inlet area (Haynes[2]). During the survey, Stages I-VII zoeae of *Pandalus tridens* (= *P. montagui tridens* Rathbun 1902) were captured in plankton tows in lower Cook Inlet. Except for Stage I, zoeae of *P. tridens* have not been described in the literature. In this report I describe and illustrate each of the seven zoeal stages captured and compare my descriptions with those of pandalid shrimp zoeae given by other authors. I also discuss the evidence from larval morphology that supports raising the subspecies, *P. montagui tridens*, to full species status, *P. tridens* Rathbun 1902. A summary of the principal morphological characteristics of described pandalid shrimp larvae of the North Pacific Ocean is also given.

METHODS

During the 1976 survey, plankton was collected by hauling 61 cm bongo samplers vertically from about 1 m above the ocean bottom to the surface at a velocity of slightly <1 m/s. Nets with 0.333 mm mesh and cod end jars with 0.571 mm mesh were used. Zoeae of *P. tridens* were collected in water 120-160 m deep about 16 km west of the Kenai Peninsula in lower Cook Inlet.

The terminology, methods of measurement, techniques of illustration, and nomenclature of gills and appendages are those used by Haynes (1979). Identification of the zoeae is based on description of Stage I zoeae hatched from known parentage by Ivanov (1971) and undescribed Stage I specimens hatched from known parentage by Ethelwyn Hoffman of the Auke Bay Laboratory's staff. Only those morphological characteristics useful for readily identifying each stage are given. For clarity, setules on setae are usually omitted from the figures, but spinulose setae are shown.

STAGE I ZOEA

Total length of Stage I zoea (Figure 1A) 3.2 mm (range 3.1-3.5 mm; 6 specimens). Rostrum slender, somewhat sinuate, without teeth, about two-thirds length of carapace, and projects horizontally. Carapace with small, somewhat angular dorsal prominence at base of rostrum and smaller

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[2]Haynes, E. 1977. IV Summary status on the distribution of king crab and pandalid shrimp larvae in Kachemak Bay-lower Cook Inlet, Alaska, 1976. *In* L. L. Trasky, L. B. Flagg, and D. C. Burbank (editors), Environmental studies of Kachemak Bay and lower Cook Inlet, vol. 4, 52 p. Alaska Dep. Fish Game, Anchorage.

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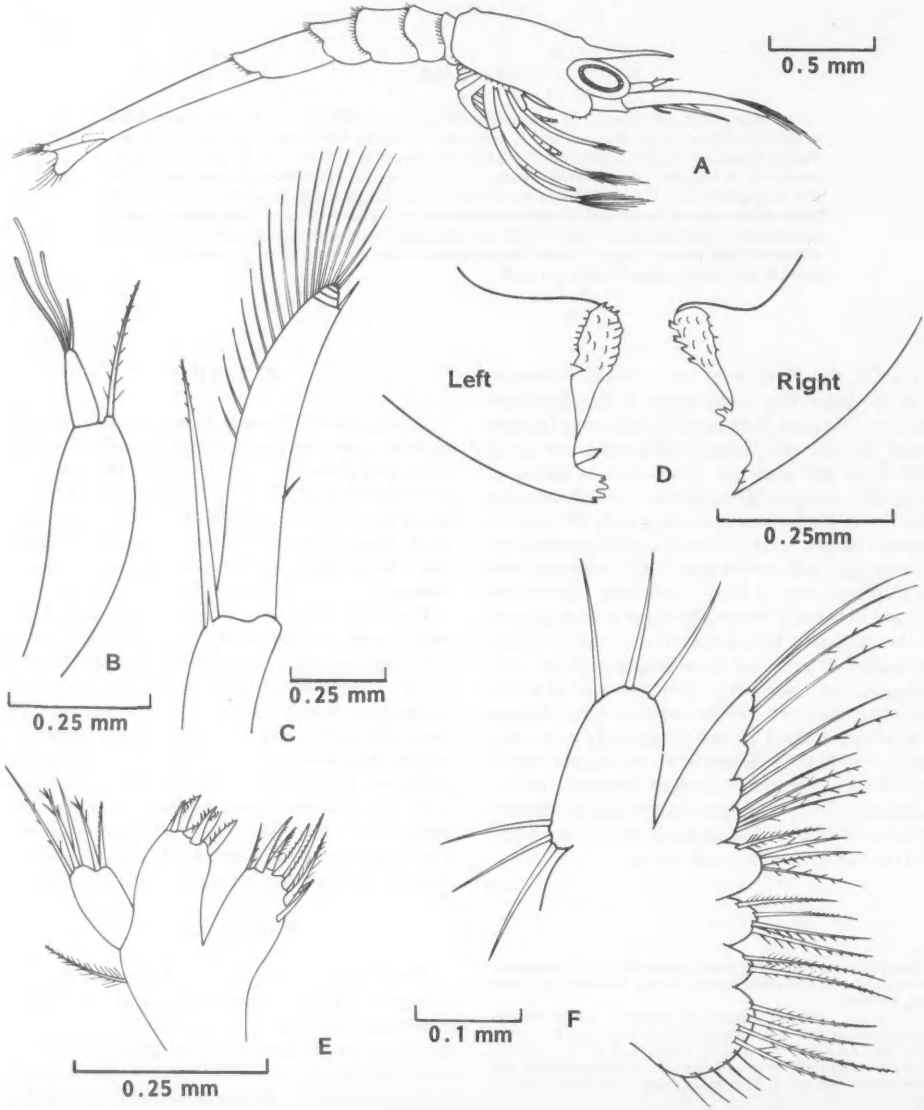
rounded prominence near posterior edge. These two prominences occur in all seven zoeal stages. Pterygostomian spines present, but minute and usually hidden by sessile eyes. Three to four minute denticles on ventral margin of carapace immediately posterior to pterygostomian spine, and about 12 somewhat larger denticles along posteroventral margin of carapace. Denticles in Stages I-III, but rarely in Stage IV. Denticles vary in number among stages and among individuals in



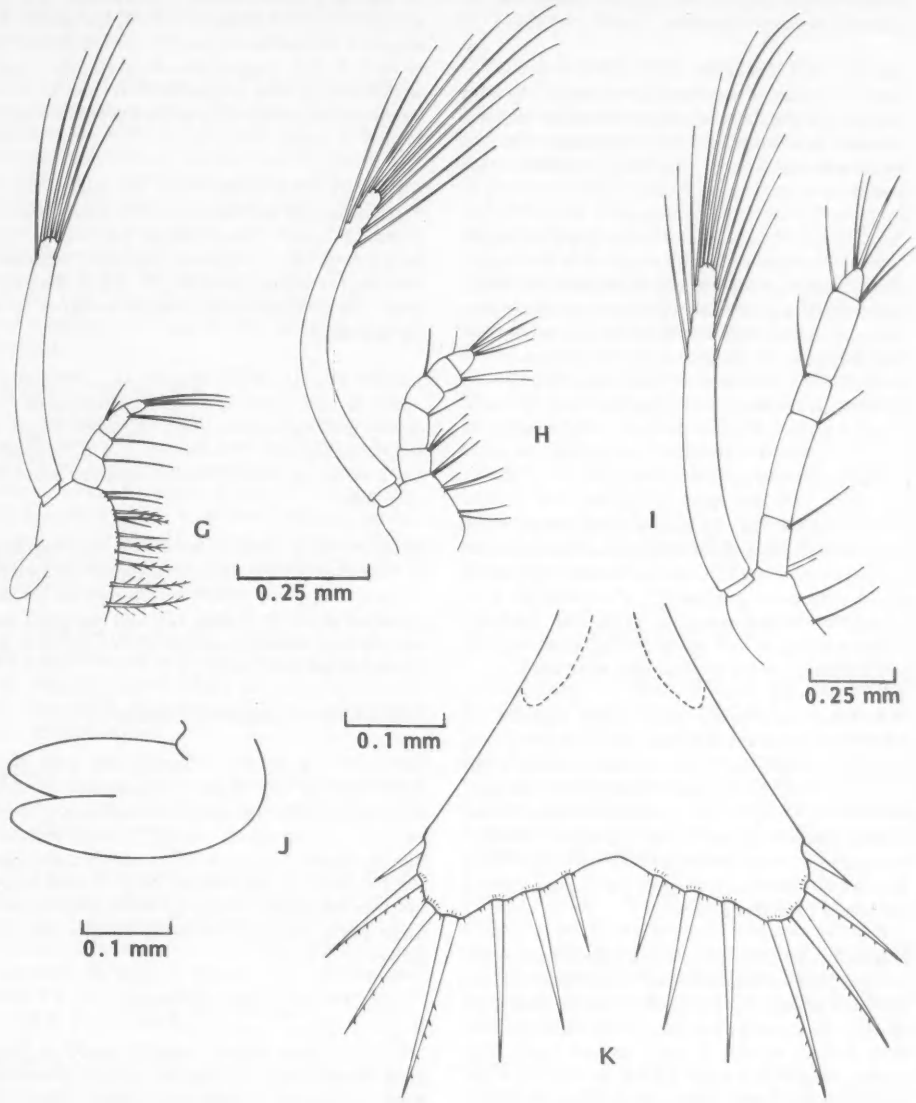


FIGURE 1.—Stage I zoea of *Pandalus tridens*: A, whole animal, right side; B, antennule, dorsal; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, dorsal; F, maxilla, dorsal; G, first maxilliped, lateral; H, second maxilliped, lateral; I, third maxilliped, lateral; J, second pereopod, lateral; K, telson, dorsal.

each stage. Posterior margins of abdominal somites fringed with spines.

ANTENNULE (Figure 1B).—First antenna, or antennule, has a simple, unsegmented, tubular basal portion; plumose seta terminally; and terminal conical projection bearing four aesthetascs: one long, one short, and two of intermediate length.

ANTENNA (Figure 1C).—Consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum spiniform, unsegmented, about three-fourths length of scale, and spinulose distally. Protopodite bears spinous seta at base of flagellum, but no spine at base of scale. Antennal scale distally divided into four joints, fringed with 17 heavily plumose setae along terminal and inner margins. Distinct seta on outer margin at base of terminal segments; another seta on outer margin, near the protopodite.

MANDIBLES (Figure 1D).—Without palps in this stage and all later zoeal stages examined. Incisor process of left mandible has six teeth in contrast to triserrate incisor process of right mandible. Left mandible bears movable premolar denticle (lacinia mobilis) and subterminal tooth only on left mandible in all zoeal stages examined.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and an endopodite. Proximal lobe (coxopodite) has seven spinulose spines terminally. Median lobe (basipodite) bears five spinulose spines and a large setose seta proximally. Endopodite originates from lateral margin of basipodite and has three terminal and two subterminal spines; two of the spines have especially long spinules.

MAXILLA (Figure 1F).—Bears platelike exopodite (scaphognathite) with six long plumose setae: three on distal margin and three on proximal margin. Endopodite has 10 nonplumose setae: 7 bear distinct setules. Basipodite and coxopodite bilobed. Basipodite bears four setae on each lobe; each seta has distinct pattern of setules. Coxopodite bears 12 setae: 2 on distal lobe and 10 on proximal lobe; 6 distal setae of coxopodite somewhat plumose, remaining 6 setae have few, if any, setules.

FIRST MAXILLIPED (Figure 1G).—Most setose of natatory appendages. Protopodite not segmented, bears 11 setae (7 of them spinulose). Endopodite distinctly four-segmented; setation formula 3, 4, 1, 1. Exopodite is long slender ramus, segmented at base; exopodite bears two terminal and four lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (Figure 1H).—Protopodite not segmented; bears seven sparsely plumose setae. Endopodite distinctly five-segmented; fourth segment expanded somewhat laterally; setation formula 5, 2, 1, 1, 3. Exopodite with two terminal, eight lateral natatory setae. No epipodite.

THIRD MAXILLIPED (Figure 1I).—Protopodite unsegmented, bears two setae. Endopodite distinctly five-segmented, about the same length as exopodite; setation formula 5, 3, 1, 1, 3. Exopodite has 2 terminal and 10 lateral natatory setae. No epipodite.

PEREOPODS.—Poorly developed, not segmented, directed under body somewhat anteriorly (Figure 1A). First three pairs biramous (second pereopod shown in Figure 1J), last two pairs uniramous and slightly smaller than pairs 1-3. All pereopods without setae.

PLEOPODS.—Absent until Stage IV.

TELSON (Figure 1K).—Continuous with sixth abdominal somite; slightly emarginate distally; bears seven pairs of densely plumose setae. Fourth pair of setae longest: length about one-half maximum width of telson. Minute spinules at base of each seta except lateral pair. A few larger spinules on distal margin between bases of four inner pairs. Enclosed uropods visible. No anal spine.

STAGE II ZOEA

Total length of Stage II zoea (Figure 2A) 4.2 mm (range 3.9-4.6 mm; 5 specimens). Rostrum without teeth, sinuate, projects somewhat dorsally. Carapace bears two prominent, supraorbital spines, one on each side of carapace; antennal and pterygostomian spines clearly visible. All zoeal stages examined except Stage I bear supraorbital, antennal, and pterygostomian spines. Epipodite slightly larger than in Stage I, but not bilobed. No

pleurobranchiae. Spines on posterior margins of abdominal somites similar in size and number to spines in Stage I.

ANTENNULE (Figure 2B).—Three-segmented; bears large lateral flagellum and smaller inner flagellum on terminal margin. Inner flagellum unsegmented, conical, and has one long spine terminally. Outer flagellum has five aesthetascs of various lengths and one plumose seta. Proximal segment bears four setae laterally near base, single seta subdistally, and two setae distally. Second segment has two setae distally. Distal segment has four plumose setae laterally near inner flagellum and has small seta laterally and subdistally.

ANTENNA (Figure 2C).—Flagellum styliform, about one-third length of scale. Antennal scale about 5½ times as long as wide and fringed along distal and inner margins with 22 long, thin plumose setae. Antennal scale still divided distally into four joints; bears two setae on lateral margin: one at base of proximal joint, one proximally. Protopodite bears spine at base of flagellum but no spine at base of scale.

MANDIBLES (Figure 2D).—Incisor processes of both mandibles more pronounced and have more teeth than in Stage I. Molar processes somewhat more developed than in Stage I, especially forward lip of truncated end.

MAXILLULE.—Similar in shape to maxillule of Stage I, except coxopodite and basipodite each bear additional spine.

MAXILLA.—Shape similar to Stage I maxilla, except scaphognathite is slightly longer proximally, bears 9-11 marginal plumose setae, and large plumose seta at proximal end. Endopodite same as endopodite of Stage I. Lobes of basipodite bear either 6 + 6 or 7 + 5 setae; lobes of coxopodite bear 3 + 11 or 3 + 12 setae.

FIRST MAXILLIPED (Figure 2E).—Epipodite of first maxilliped longer than in Stage I. Setation formula of endopodite 3, 2, 1, 3. Protopodite unsegmented, bears about 20 setae.

SECOND MAXILLIPED.—Same as Stage I, except each segment of endopodite may have an additional seta.

THIRD MAXILLIPED.—Dactylopodite (Figure 2F) narrower, longer than in Stage I.

FIRST AND SECOND PEREOPODS (second pereopod shown in Figure 2G).—Endopodites of first and second pereopods functionally developed, five-segmented and terminating in simple conical dactylopodite. Exopodite of first pereopod is longest exopodite of pereopods. Exopodites of first and second pereopods have two terminal and eight lateral natatory setae.

THIRD PEREOPOD (Figure 2H).—Exopodite and endopodite nonfunctional but segmented at base. Endopodite tipped by four simple setae.

FOURTH AND FIFTH PEREOPODS (Figure 2I).—Poorly developed, unsegmented, and without exopodites.

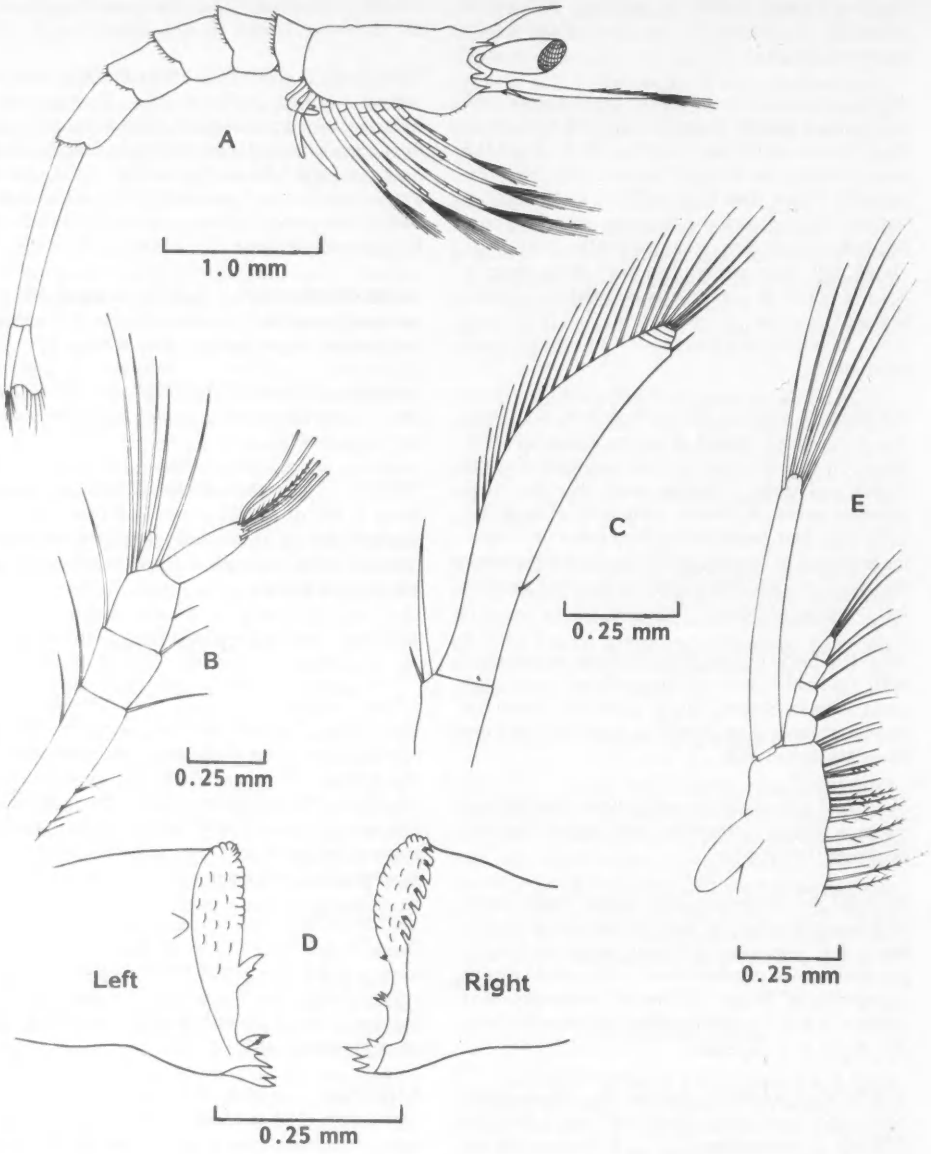
TELSON (Figure 2J).—Telson similar in shape to Stage I, but distinctly segmented from sixth abdominal somite. Telson has eight pairs of densely plumose setae. Uropods still enclosed. Anal spine present but minute.

STAGE III ZOEA

Total length of Stage III zoea 5.9 mm (range 5.6-6.3 mm; 7 specimens). No change in shape of rostrum from Stage II. Spines along anteroventral and posteroventral margin of carapace still present, but minute and fewer than in Stage II. Epipodite on first maxilliped still only gill structure present. Spines on posterior margins of abdominal somites smaller than in Stage II.

ANTENNULE.—Similar in shape to antennule of Stage II but bears several additional setae; a spine projects downward from ventral surface of proximal segment. From this stage on, change in antennule slight: inner flagellum lengthens, more setae on antennule.

ANTENNA.—Flagellum styliform, two-segmented, still only about one-third length of scale. Antennal scale about six times as long as wide; two complete joints at tip (Figure 3A). Terminal spine on lateral margin of scale does not quite reach tip of scale. Protopodite bears small spine at base of flagellum and minute projection at base of scale.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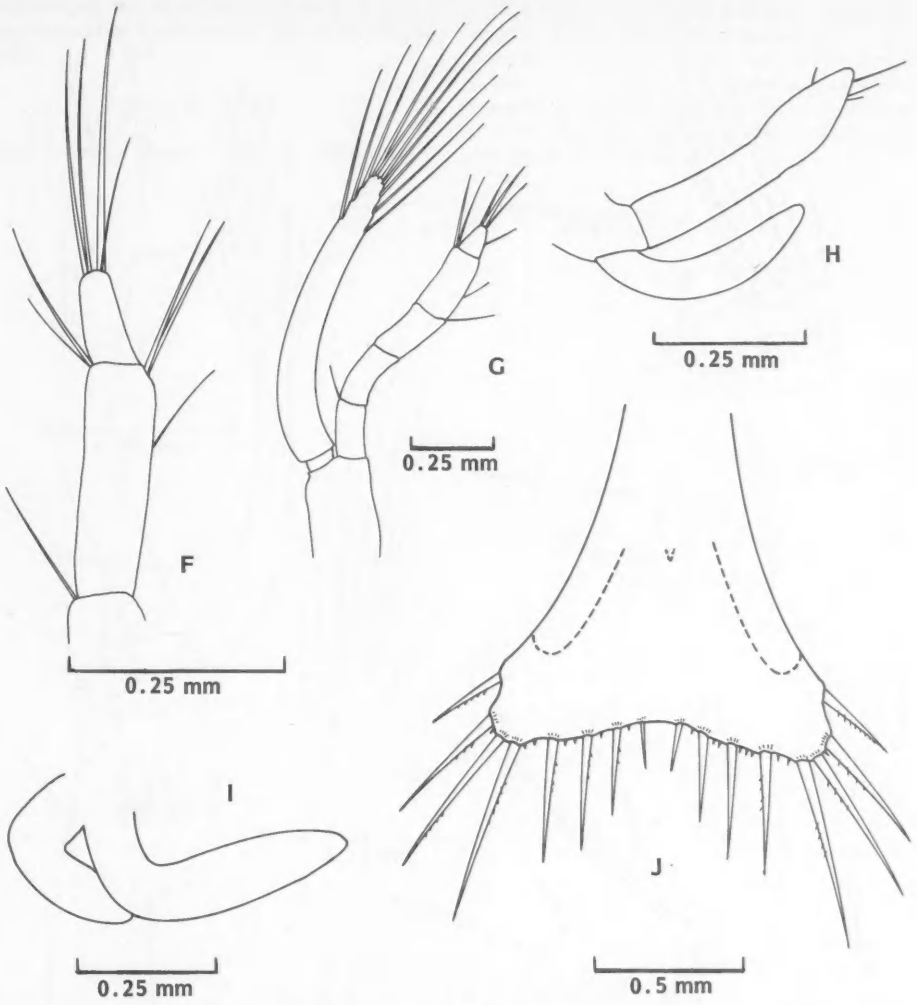

FIGURE 2.—Stage II zoea of *Pandalus tridens*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles (left and right), posterior; E, first maxilliped, lateral; F, third maxilliped (distal segments), lateral; G, second pereopod, lateral; H, third pereopod, lateral; I, fourth and fifth pereopods, lateral; J, telson, dorsal.

FIRST AND SECOND PEREOPODS.—Essentially same as Stage II, except exopodite of second pereopod bears additional pair of setae.

THIRD PEREOPOD (Figure 3B).—Functional, five-segmented. Exopodite bears two terminal and eight lateral natatory setae.

FOURTH PEREOPOD (Figure 3C).—Functional. Dactylopodite tipped by spine and simple seta.

FIFTH PEREOPOD.—Similar to fourth pereopod except terminal spine not as fully developed.

TELSON (Figure 3D).—Uropods free. Endopodite

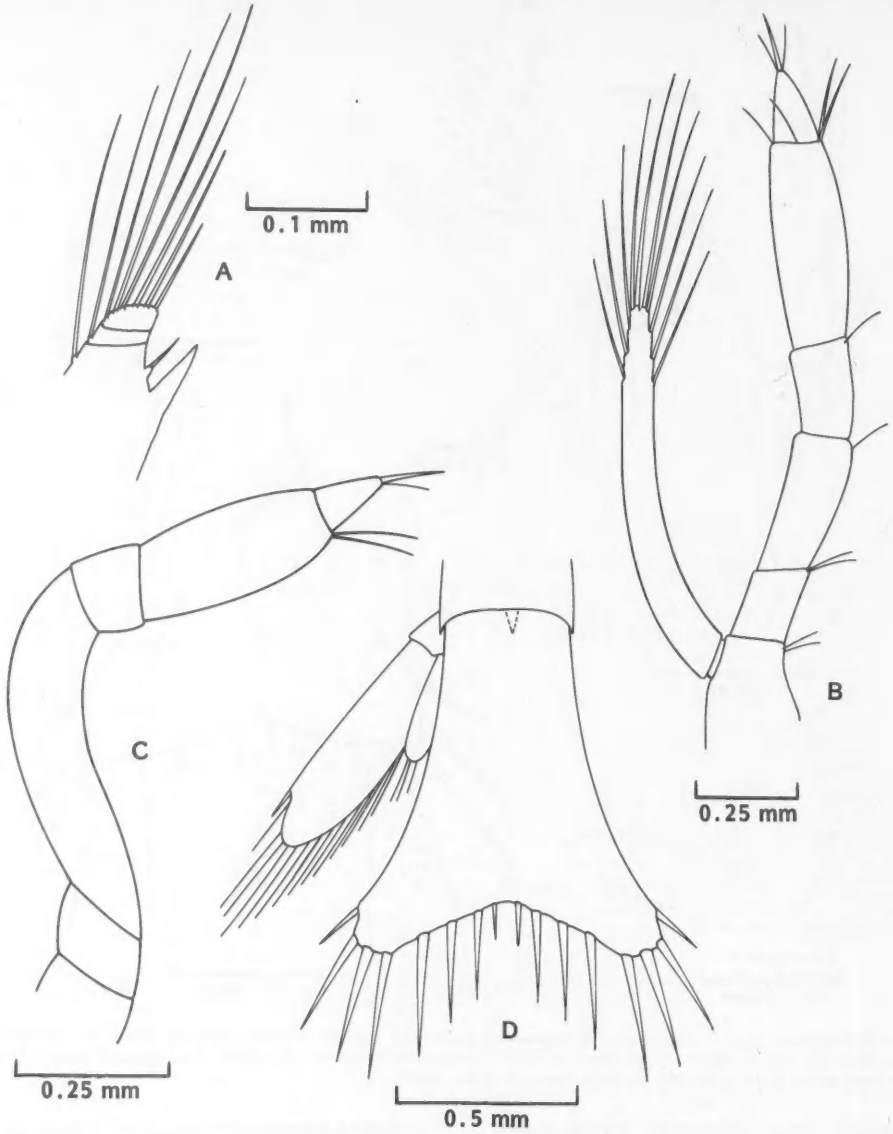

FIGURE 3.—Stage III zoea of *Pandalus tridens*: A, antennal scale (distal portion), ventral; B, third pereopod, lateral; C, fourth pereopod, lateral; D, telson, dorsal.

undeveloped, less than one-half length of exopodite, bears three setae distally. Anal spine clearly visible.

STAGE IV ZOEA

Total length of Stage IV zoea 7.8 mm (range 7.0-8.4 mm; 9 specimens). Rostrum (Figure 4A) projects horizontally but curves slightly downward at tip, bears two teeth at base. A few minute spines still on anteroventral and posteroventral margins of carapace. Epipodite of first maxilliped bilobed. Posterior margins of abdominal somites fringed as in Stage III.

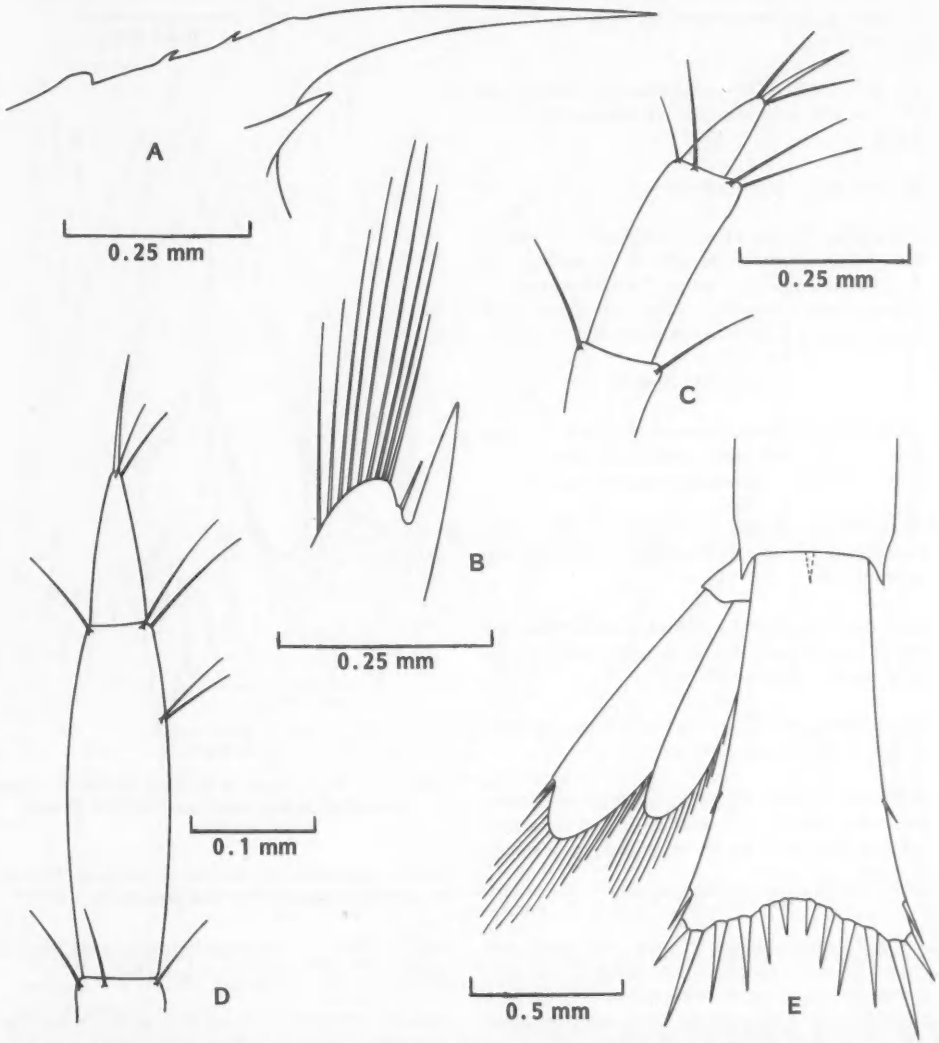

FIGURE 4.—Stage IV zoea of *Pandalus tridens*: A, rostrum, right side; B, antennal scale (distal portion), ventral; C, second pereopod (terminal segments), lateral; D, third pereopod (distal segments), lateral; E, telson, dorsal.

ANTENNA.—Flagellum still styliform, only about one-third length of scale. Antennal scale about seven times as long as wide, no joints at tip; terminal spine projects considerably beyond tip of scale (Figure 4B). Protopodite bears small spine at base of flagellum and antennal scale.

SECOND PEREOPOD.—Distal joint of propodite (Figure 4C) widened, projects distally in later stages.

THIRD PEREOPOD.—Dactylopodite lengthened (Figure 4D); exopodite has an additional pair of setae.

PLEOPODS.—Minute buds.

TELSON (Figure 4E).—Endopodite of uropod about three-fourths length of exopodite and fringed with about 15 setae. Lateral margins of telson widen posteriorly, have two spines each. Distal margin emarginated, bears 6 + 6 spines.

STAGE V ZOEA

One specimen with rostrum broken and exopodites of third pereopods missing. Posterior margins of abdominal somites minutely fringed.

ANTENNA.—Flagellum slightly rounded at tip, two-thirds length of antennal scale, five-segmented.

SECOND PEREOPOD.—Chela partially formed; distal joint of propodite projected somewhat distally, tipped by spine (Figure 5A).

SECOND PLEOPODS.—About one-fourth height of second abdominal somite.

TELSON (Figure 5B).—Uropods fully developed, no evidence of transverse hinge. Lateral margins somewhat parallel but widen slightly posteriorly.

STAGE VI ZOEA

Total length of Stage VI zoeae 10.7 mm (range 10.2-11.2 mm; 2 specimens). Rostrum (Figure 6A) about one-third length of carapace, projects horizontally, bears six teeth dorsally, tip bears hump indicating future location of distal tooth. A few minute spines on posterior margin of fifth somite.

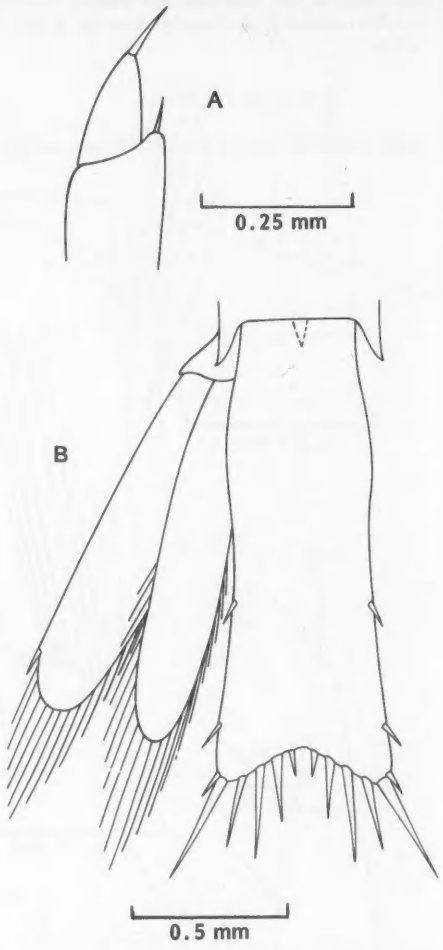

FIGURE 5.—Stage V zoea of *Pandalus tridens*: A, second pereopod (distal segments), lateral; B, telson, dorsal.

Bud of epipodite on second maxilliped. Pleurobranchiae at base of all five pereopods.

ANTENNA.—Inner flagellum nearly as long as antennal scale, about 25-segmented.

SECOND PEREOPOD.—Chela well formed (Figure 6B). Terminal spines of propodite and dactylopodite each bear single spine at base.

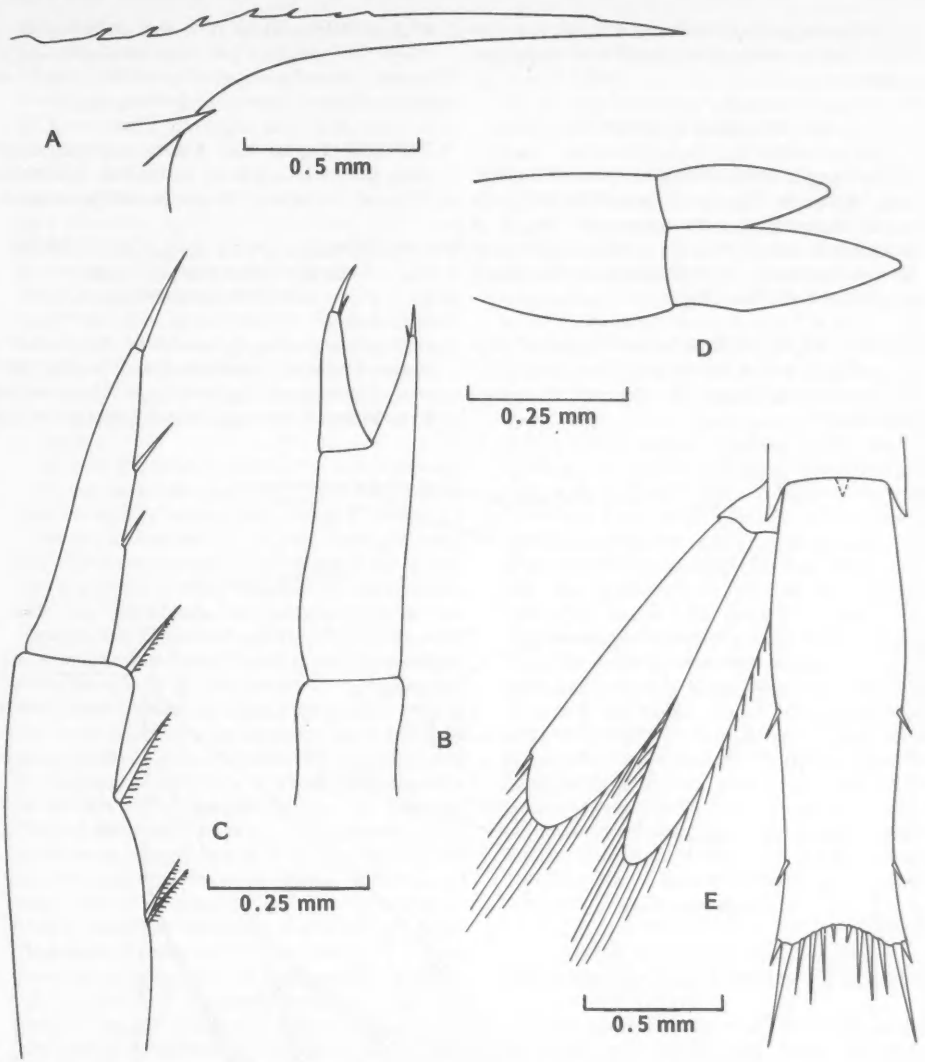

FIGURE 6.—Stage VI zoea of *Pandalus tridens*: A, rostrum, right side; B, second pereopod (distal segments), lateral; C, third pereopod (distal segments), lateral; D, second pleopod, lateral; E, telson, dorsal.

THIRD PEREOPOD.—Dactylopodite well developed; has two distinct spines along inner margin (Figure 6C).

PLEOPODS.—Pleopods segmented at base; no setae or appendices internae. Second pleopod about one-half height of second abdominal somite (Figure 6D).

TELSON (Figure 6E).—Lateral margins somewhat parallel, but not as much as in Stage VII; each margin bears two spines. Posterior margin

slightly emarginated and bears 6 + 6 spines distally. Transverse hinge of exopodite of uropod not evident.

STAGE VII ZOEA

Total length of Stage VII zoea 13.0 mm (1 specimen). Rostrum (Figure 7A) curved slightly upward, slightly less than one-half length of carapace; bears seven teeth dorsally, tooth near tip not developed. No change in number of gill structures from Stage VI.

SECOND PEREOPOD.—Terminal spine of dactylopodite may bear two spines at base instead of one spine, as in Stage VI; carpopodites unsegmented.

PLEOPODS.—Exopodite and endopodite of pleopods tipped by a few setae; no appendices internae. Second pleopod (Figure 7B) about two-thirds height of second abdominal somite.

TELSON (Figure 7C).—Lateral margins essentially parallel, each bears two spines. Transverse hinge of exopodite of uropod partially complete.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

The only previously published description of larvae of *Pandalus tridens* is that of Ivanov (1971) who described and figured Stage I zoeae reared from known parentage. My description of the

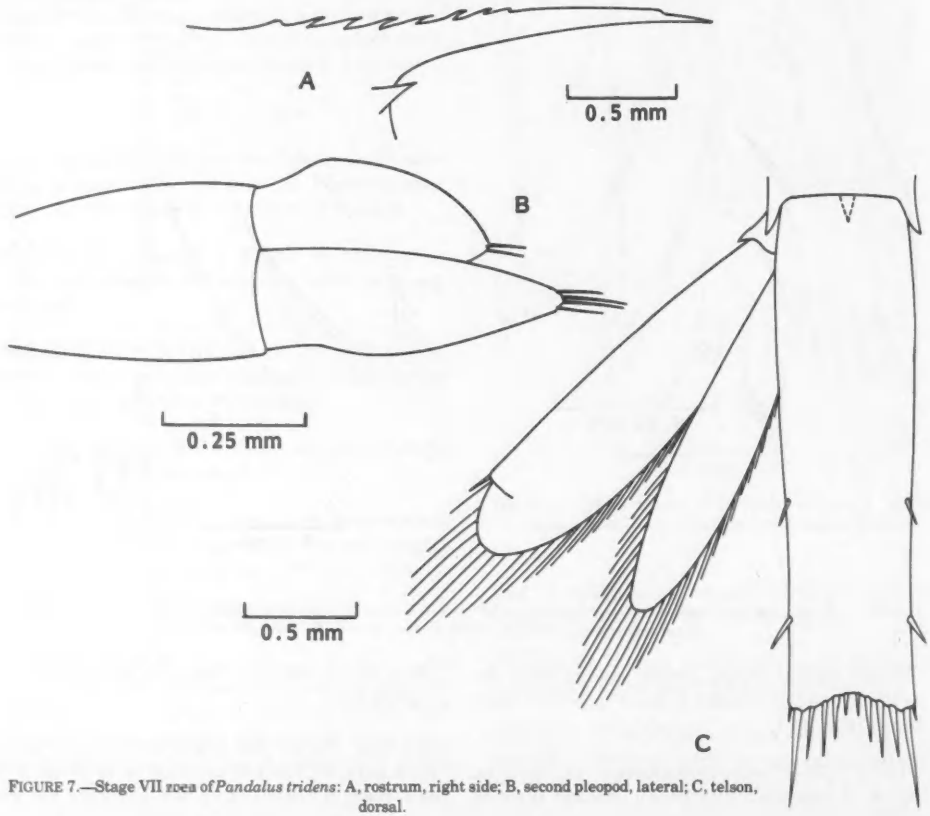

FIGURE 7.—Stage VII zoea of *Pandalus tridens*: A, rostrum, right side; B, second pleopod, lateral; C, telson, dorsal.

Stage I zoeae agrees in all essential aspects with Ivanov's description.

Larvae of *P. tridens* are similar to larvae of *P. borealis*, *P. goniurus*, *P. jordani*, and *P. stenolepis*: all have poorly developed pereopods and exopodites on pereopods 1-3 in Stage I. Larvae of *P. borealis* (described by Haynes [1979]), and *P. goniurus* (described by Haynes [1978]), and *P. jordani* (described by Modin and Cox [1967]) are readily distinguishable from larvae of *P. tridens* by the lack of spines on the posterior margins of the abdominal somites and by the rostrum, which in early stages is spiniform and projects downward rather than being sinuate and projecting upwards as in *P. tridens*. In addition, the antennal scales of larvae of *P. borealis*, *P. goniurus*, and *P. jordani* are markedly shorter and wider than in larvae of *P. tridens*.

Zoeae of *P. tridens* described in this report are most similar to zoeae of *P. stenolepis* described by Needler (1938), especially in Stage I. In Stage I zoeae of both species the carapace bears denticles, the abdominal somites are fringed with spines, and the antennal scale is relatively long and narrow. The Stage I zoeae of these species differ: the carapace and abdominal somites of Stage I zoeae of *P. stenolepis* are flared laterally, and the antennal scale bears 9-12 plumose setae; the carapace and abdominal somites of Stage I zoeae of *P. tridens* are not flared, and the antennal scale bears 17 plumose setae. Also, the telson of Stage I zoeae of *P. stenolepis* is considerably wider and the posterior margin more emarginate than the telson of Stage I zoeae of *P. tridens*. Other morphological differences between zoeae of the two species are the antennal flagellum and rostrum. The antennal flagellum in all zoeal stages of *P. stenolepis* is longer than the antennal scale; the antennal flagellum of zoeae of *P. tridens* remains shorter than the antennal scale through at least Stage V. The rostrum of *P. stenolepis* zoeae is as long as, or longer than, the carapace and bears teeth as early as Stage II; the rostrum of *P. tridens* zoeae remains shorter than the carapace as late as Stage VII and does not bear teeth until Stage IV.

The morphology of Stages I-VII zoeae of *P. tridens* from lower Cook Inlet confirms the opinion (Ivanov 1971; Squires[3]) that *P. montagui tridens*, the Pacific subspecies of *P. montagui* Leach, should be given the full specific rank of *P. tridens* Rathbun 1902. Rathbun's (1902, 1904) separation of the Pacific subspecies, *P. montagui tridens*, from the Atlantic species, *P. montagui*, was based on slight differences in adult morphology. For instance, the rostrum of the Pacific subspecies was 1½-1⅔ times the length of the carapace compared with 1²/₅-1½ times the length of the carapace for the Atlantic species. Also, termination of the dorsal rostral spines of the Pacific subspecies was behind the middle of the carapace rather than in the middle or in front of the middle of the carapace as in the Atlantic form. Squires' (see footnote 3) conclusion that the Pacific subspecies should be given specific status was based on coloration of adults. Ivanov's (1971) conclusion was based on morphological differences between Stage I larvae of *P. tridens* from the Gulf of Alaska and Pike and Williamson's (1964) description of Stage I larvae of *P. montagui* from the North Atlantic. In Stage I *P. montagui* the margins of the carapace and abdominal somites are smooth; in Stage I *P. tridens* the carapace bears pterygostomian spines, the antero- and posterolateral margins of the carapace bear denticles, and the posterior margins of the abdominal somites bear minute spines. In *P. tridens*, the rostrum is longer and the number of setae and spines on the antennal scale is greater than in *P. montagui*. Also, *P. tridens* larvae are larger than larvae of *P. montagui*. My comparison of the seven zoeal stages of *P. tridens* from Cook Inlet with the zoeae of *P. montagui* raised in the laboratory and collected from North Atlantic plankton by Pike and Williamson (1964) confirms the morphological differences found by Ivanov (1971) for Stage I and shows that these differences persist through later stages.

SUMMARY OF PRINCIPAL MORPHOLOGICAL CHARACTERISTICS

Certain characteristics of larvae of pandalid shrimp from the North Pacific Ocean change form as the larvae develop. I discuss changes of these characteristics and categorize the larvae by number of stages. I also discuss the probable morphology of larvae of *Pandalopsis ampla* Bate, *P. aleutica* Rathbun, and *P. longirostis* Rathbun and larvae tentatively identified as *Dichelopandalus leptocerus* (Smith).

Although the number of pereopods bearing exopodites does not change during larval development, the exopodites themselves degenerate

[3]Squries, H. J. 1965. Decapod crustaceans of Newfoundland, Labrador and the Canadian Eastern Arctic. Fish. Res. Board Can., MS Rep. Ser. Biol. 810:1-212. Biological Station, Nanaimo, B.C. V9R-5K6.

during later stages, usually at the molt to the megalopa. In Table 1, poorly developed pereopods in Stage I are unsegmented pereopods that are directed anteriorly under the cephalothorax. Usually pereopods become functional by Stage III.

Denticles on the carapace and spines on the abdominal somites are most prevalent in Stage I and tend to disappear during larval development. Thus, in *Pandalus platyceros* most of the denticles and spines have disappeared by Stage III; in *P. stenolepis* and *P. tridens* most have disappeared by Stage VI.

For most pandalid shrimp larvae, the typical number of telsonic spines is 7 + 7 in Stage I and 8 + 8 in later stages. In the latest stage another pair may be added. The total number of telsonic spines of *P. kessleri* varies from 30-34 (Stage I) to 14-15 (Stage V); *Pandalopsis coccinata* has 55-56 telsonic spines in Stage I (Kurata 1955, 1964). Stage I *Pandalus kessleri* and *Pandalopsis coccinata* usually have 16 + 16 and 28 + 28 telsonic spines, respectively (Table 1).

The number of larval stages of *Pandalopsis dispar*, *P. coccinata*, *Pandalus tridens*, and *P. jordani* has not been verified. Seven zoeal stages are known for *Pandalopsis dispar* and *Pandalus tridens*. Based on morphological development, Stage VII of *Pandalopsis dispar* is probably the last larval stage. *Pandalus tridens* probably has an additional stage before the larvae molt to the first juvenile stage. Only the first zoeal stage of *Pandalopsis coccinata* is known, but development of this stage is so far advanced that only one or, at the most, two more stages probably appear before the larvae molt to the first juvenile stage. For *Pandalus jordani*, I have estimated six larval stages based on development of larvae of morphologically similar species, *P. borealis*, *P. goniurus*, and *P. tridens*, rather than the 11-13 stages obtained by Modin and Cox (1967) or the 8+ stages obtained by Lee (1969) in the laboratory. Modin and Cox (1967) noted that the 11-13 larval stages of *P. jordani* obtained by them in the laboratory were nearly twice the number of larval stages of the closely related *P. borealis*. Artificial laboratory conditions may have caused a greater number of larval stages than natural conditions.

The numbers of larval stages cited in Table 1 include the megalopa stage because the transition from zoea to megalopa is not always abrupt and may extend over several molts. For example, *P. hypsinotus* has functional pleopods in Stage VII, but other morphological characteristics normally associated with postzoea occur earlier (Haynes 1976). Also, the number of larval stages of some species vary slightly depending on geographical origin. Larvae of *P. hypsinotus*, *P. goniurus*, and *P. borealis* from the western North Pacific Ocean and *P. borealis* from British Columbia waters have one or two more stages than larvae of these species from Alaskan waters (Haynes 1976, 1978, 1979). Geographical variation in larval morphology has not been verified for other species of pandalids from the North Pacific.

The number of larval stages given in Table 1 refers to development in the sea rather than in the laboratory. Development in the laboratory often results in molt retardation and extra stages. Although the number of molts required to reach a specific point in development may vary in wild pandalid shrimp (Haynes 1978), the stages are, for the most part, remarkably constant and limited in number (Gurney 1942).

For identification purposes, pandalid shrimp larvae of the North Pacific Ocean can be categorized into two groups on the basis of morphological

TABLE 1.—Principal morphological characteristics and number of larval stages of known larvae of pandalid shrimp of the North Pacific Ocean. + = yes; − = no. (Only the most complete references on larval morphology are given.)

Species	Pereopods bearing exopodites	Pereopods poorly developed in Stage I	Spines on abdominal somites	Denticles on carapace margin	No. of telson spines in Stage I	No. of larval stages	References[1]
Pandalopsis coccinata	1-2	−	−	−	28 + 28	3	4
P. dispar	1-2	−	−	−	12 + 12	7	1
Pandalus kessleri	1-2	−	−	−	16 + 16	4	3, 4
P. danae	1-2	−	−	−	7 + 7	6	1
P. hypsinotus	1-2	−	−	−	7 + 7	7	1, 10
P. platyceros	1-3	−	+	+	8 + 8	5	1, 9
P. tridens	1-3	+	+	+	7 + 7	8	8, 13
P. stenolepis	1-3	+	+	+	7 + 7	6	2
P. borealis	1-3	+	−	−	7 + 7	6	1, 4, 12
P. goniurus	1-3	+	−	−	7 + 7	6	5, 11
P. jordani	1-3	+	−	−	7 + 7	6	6, 7

[1]References: 1) Berkeley (1930); 2) Needler (1938); 3) Kurata (1955); 4) Kurata (1964); 5) Ivanov (1965); 6) Modin and Cox (1967); 7) Lee (1969); 8) Ivanov (1971); 9) Price and Chew (1972); 10) Haynes (1976); 11) Haynes (1978); 12) Haynes (1979); 13) this report.

characteristics: species with exopodites on pereopods 1-3 and species with exopodites only on pereopods 1 and 2. Species with exopodites on pereopods 1 and 2 are characterized by well-developed pereopods in Stage I, and no spines on the abdominal somites or denticles on the carapace margin. For three of the species with exopodites on pereopods 1 and 2 (*Pandalopsis coccinata*, *P. dispar*, and *Pandalus kessleri*), the numbers of telsonic spines in Stage I are considerably greater than for species with exopodites on pereopods 1-3.

Fewer thoracic exopodites usually indicate fewer stages before the megalopa (Pike and Williamson 1964). This is not always true for pandalid shrimp larvae of the North Pacific Ocean. For instance, larvae of *P. danae*, *P. hypsinotus*, and *Pandalopsis dispar* also bear exopodites on first and second pereopods; but, the number of their larval stages is 6, 7, and 7, respectively. Also, Stage I larvae of *P. dispar* have dorsal and ventral teeth on the rostrum, 12 + 12 spines on the telson, and a long, jointed antennal flagellum that is about six times the length of the antennal scale; but the pleopods are not tipped with setae until Stage V, and Stage VII zoeae still bear a supraorbital spine.

A greater number of telsonic spines in Stage I is associated with fewer larval stages in development of the Caridea (Gurney 1942; Pike and Williamson 1964). This is true for *Pandalus platyceros*, *P. kessleri*, and *Pandalopsis coccinata*, which have 8 + 8, 16 + 16, and 28 + 28 telsonic spines in Stage I and 5, 4, and 3 larval stages, respectively. An exception is *P. dispar*, which has 12 + 12 telsonic spines in Stage I, but may have as many as seven larval stages.

Four species of pandalid shrimp in the North Pacific Ocean are not listed in Table 1: *Pandalopsis ampla*, *P. aleutica*, *P. longirostris*, and *Dichelopandalus leptocerus*. Larvae of *P. ampla*, *P. aleutica*, and *P. longirostris* have not been described. If larvae of *P. ampla*, *P. aleutica*, and *P. longirostris* undergo typical development of larvae of the genus *Pandalopsis* (Kurata 1964; Berkeley 1930), they will be characterized by advanced development, especially their large size and long antennal flagellum. Stage I *Pandalopsis* spp. larvae are at least 10.0 mm long and the antennal flagellum is longer than the body and segmented throughout its length. For comparison, Stage I larvae of *Pandalus* are 8.0 mm or less in length and the antennal flagellum is usually unsegmented and shorter than the length of the carapace. Stage I and II larvae of *D. leptocerus* have been tentatively identified from western Greenland waters (Pike and Williamson 1964). The larvae identified as *D. leptocerus* are most similar to larvae of *P. stenolepis* and *P. platyceros*: in Stage I and II, *D. leptocerus*, *P. stenolepis*, and *P. platyceros* bear prominent denticles on the anteroventral margin of the carapace, the anteroventral margin of the carapace and posterior margin of the third abdominal somite are flared, the rostrum is about as long as the carapace, and exopodites are present on pereopods 1-3. Larvae of *D. leptocerus* can be distinguished, however, from the identified pandalid shrimp larvae of the North Pacific Ocean, including larvae of *P. stenolepis* and *P. platyceros*, by the presence of posterolateral spines on the fifth abdominal somite.

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SPAWNING INCIDENCE AND BATCH FECUNDITY IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*[1]

J. ROE HUNTER[2] AND STEPHEN R. GOLDBERG[3]

ABSTRACT

Histological criteria were developed to age postovulatory follicles from examination of laboratory-spawned northern anchovy and used to estimate the frequency of spawning of natural populations. One-day-old, postovulatory follicles were the preferred estimator of spawning frequency; 48 hours after spawning postovulatory follicles could not be consistently identified because of their rapid degeneration; and the occurrence of postovulatory follicles less than 24 hours old was affected by hour of sampling and sexual composition of the school. The nightly spawning incidence was estimated to be 16±4% of the northern anchovy population in February and 12% in March. Thus, females spawned about every 6-8 days during the peak of the breeding season. The rate of oocyte development corresponded with this reproductive rate, indicating that a new mode of yolked oocytes matured about once a week. Nearly all eggs in the most advanced mode in the ovary were spawned in one night and the number of eggs spawned was estimated to be 389±59 eggs/g of female (ovary-free wet weight). The high spawning frequency and the prolonged breeding season of the northern anchovy indicate that total fecundity may be limited by food availability and energy reserves.

Ichthyoplankton surveys have become one of the standard methods for estimating biomass of marine fish populations. At high latitudes many fishes produce a single spawning batch per year (Qasim 1956) and spawning biomass may be directly estimated from total fecundity and production of eggs and larvae. Multiple (fractional) spawning fishes are characteristic of subtropical and tropical seas (Nikolsky 1963) and estimation of spawning biomass from egg and larval production is dependent upon the number of spawnings per year and the number of eggs per spawning. At present, no adequate method exists for estimating these two parameters for pelagic, multiple spawning fishes.

Past methods have employed measurements of size-frequency distribution of yolked oocytes (usually eggs >0.2 mm in diameter). Eggs are often distributed in one to three modes and the number of eggs in the most advanced mode has been assumed to be equal to the number of eggs produced per spawning (Clark 1934; MacGregor 1968). Another approach has been to count all yolked oocytes in reproductively active females and to assume that these are equal to the number of eggs spawned in a season (Macer 1974). Neither approach provides conclusive evidence for the number of spawnings nor total egg production. All eggs in the most advanced mode may not ovulate (Clark 1934; Yamamoto and Yamazaki 1961) and atresia may reduce the number of eggs per spawning (Macer 1974; Ivankov 1976). Further, the total number of yolked oocytes may not provide an estimate of total fecundity because some of the small unyolked oocytes, not included in such counts, could mature later during the same breeding season.

It has long been known in teleost fishes (Cunningham 1898) that at ovulation a remnant of the ovulated follicle (empty or postovulatory follicle) remains in the ovary. Postovulatory follicles are believed to be transitory because of their rarity in field-collected material (Wheeler 1924; Yamamoto 1956; Gokhale 1957; DeVlaming 1972; Goldberg 1977; Andrews[4]), but actual measurements of their longevity are rare because the time of spawning must be known. Yamamoto and Yoshioka (1964), using *Oryzias latipes* which spawns every 3 days, reported postovulatory follicles were barely distinguishable on the third day after spawning. They suggested that the frequency of spawning

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[4]Andrews, C. B. 1931. The development of the ova of the California sardine (*Sardina caerulea*). Unpubl. manuscr., 88 p. Stanford University, Stanford, CA 94305.

could be determined by the presence of postovulatory follicles but the estimate would have to be made soon after spawning. Through techniques of Leong (1971) it was possible to induce spawning in the northern anchovy, *Engraulis mordax*, in the laboratory, making it possible to characterize the histological degeneration of postovulatory follicles on a time basis. Thus, it seemed feasible that spawning frequency of natural populations of *E. mordax* could be estimated from incidence of postovulatory follicles in females once the period in which they could be detected was established. Moreover, once recently spawned fish were identified, the rate of maturation of subsequent egg batches as well as the number of eggs produced per batch could be estimated.

The objectives of this study were to establish the detection period for postovulatory follicles in northern anchovy and to estimate the incidence of natural spawning through histological examination of these structures. In addition, by using this information to guide our selection of specimens, we provide a new estimate of the number of eggs released per spawning or batch fecundity, and the time required for subsequent spawnings. Previous estimates for anchovy based on frequency distributions of yolked oocytes include those of MacGregor (1968) and Norberg.[5]

[5]Norberg, R. H. 1975. Investigations on the fecundity of northern anchovy, jack mackerel and Pacific mackerel. Unpubl. manuscr., 23 p. Calif. Dep. Fish Game, 350 Golden Shore, Long Beach, CA 90802.

METHODS

The period over which postovulatory follicles can be detected in the ovary was determined from anchovy held in the laboratory. Groups of anchovy reared to sexual maturity were induced to spawn using the method of Leong (1971). A total of 119 females were sampled; fish were killed at the time of spawning and thereafter at 24-h intervals up to 9 days after spawning. Ovaries were fixed in Bouin's fixative or 10% neutral buffered Formalin[6] and embedded in Paraplast. Histological sections were cut at 6 μm and stained with Harris' hematoxylin followed by eosin counterstain, Masson's trichrome, periodic acid-Schiff reagent, or Heidenhain's iron hematoxylin. A classification system for postovulatory follicles was established and laboratory specimens were classified without prior knowledge of their age to estimate the accuracy of the technique. Field samples were then classified using the same criteria. Three field collections of anchovy females from the Southern California Bight were examined to determine the frequency of spawning in natural populations: 3 commercial purse seine samples of 38-65 females each from March 1977; 4 research trawl samples of 1-11 females from September 1977; and 29 research trawl samples of 10 or 11 females from February 1978 (Figure 1).

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

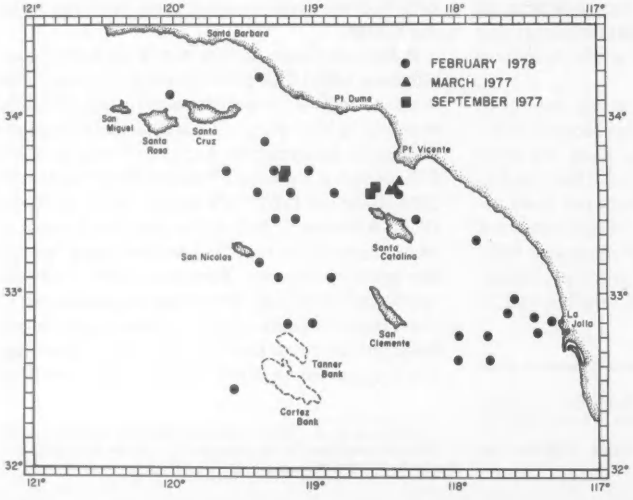

FIGURE 1.—Location of samples of female northern anchovy taken off southern California in March and September 1977 and February 1978.

The number of eggs per mode was estimated for 117 of the field-caught specimens by fixing a weighed sample in Gilson's fluid and determining the size-frequency distribution of yolked oocytes (MacGregor 1968; Macer 1974). One-hundred and fifty of the oocytes >0.20 mm on the major axis were measured to the nearest 0.05 mm from each sample and all the remaining oocytes (>0.20 mm) were counted. We shall use "diameter" to refer to these measurements but since anchovy eggs are longer than wide, it is not a diameter in a strict sense but the major axis of an oblate spheroid.

The form of the distribution of egg diameters within an ovary was similar to those illustrated for other multiple spawning fishes (Macer 1974). Distributions varied from ones composed of two to three distinct modal groups of eggs to ones with only a single mode. Even in those with very distinct modal groups the tails of adjacent modes often overlapped. We used the program NORMSEP (Abramson 1971) to separate modal groups, estimate the mean egg diameter within a mode, and estimate iteratively the number of eggs within a mode. Although one must arbitrarily assume egg diameters within a mode are normally distributed, the program does eliminate some of the subjectivity in judging the range of diameters to include within a mode and how the tails of adjacent modes should be proportioned.

Just prior to ovulation and spawning the modal group of eggs about to be spawned takes up fluid and swells to three or four times its former volume (Fulton 1898). These hydrated eggs greatly increase the ovary weight and increase the total weight of the female. To avoid this bias in female weight we used female weight less ovary weight (ovary-free wet weight) to express fecundity-weight relations. We also provide fecundity estimates based on total weight in tabular form so that conversions can be made if desired.

CLASSIFICATION OF OVARIES

Ovaries of laboratory matured females that had spawned within 24 h in all cases contained postovulatory follicles. They were similar in appearance to those described for a variety of teleosts (Cunningham 1898; Wheeler 1924; Bowers and Holliday 1961; Yamamoto and Yoshioka 1964; Moser 1967; Scott 1974). In specimens killed 0-6 h after spawning, postovulatory follicles consisted of irregularly shaped structures composed of columnar follicle cells and an underlying connective tissue theca (Figure 2A, B). In some cases the columnar cells had hypertrophied slightly. The lumen characteristically contained eosinophilic granules of uncertain origin.

Degeneration was pronounced in material examined 24 h after spawning. The postovulatory follicle (Figure 2C) had greatly shrunken or collapsed on itself, vacuoles had become common, and walls of the follicle cells were no longer distinguishable (Figure 2D). The granular material that was observed in postovulatory follicles taken at the time of spawning was still present but not as abundant. The prominent underlying connective tissue theca seen in new postovulatory follicles was no longer distinct. Degeneration had progressed further, 48 h after spawning. The follicle was one-half to one-fourth smaller than at 24 h, the lumen was very small or indistinguishable, eosinophilic granules were absent, and nuclear sizes were greatly reduced.

Owing to their rapid degeneration, postovulatory follicles were difficult to age in laboratory specimens sampled 48 h after spawning. At this time they may be confused with intermediate stages of atretic oocytes (Lambert 1970). On the other hand, classification of postovulatory follicles into age 0 day and age 1 day was done with an accuracy of 76 to 84% (Table 1). In view of this, the following system was established for classification of ovaries from field-caught specimens:

Hydrated: ovaries with many hydrated eggs (eggs enlarged by fluid uptake just prior to ovulation) and no postovulatory follicles. (Spawning considered to be imminent.)

Age 0 day: new postovulatory follicles, showing no sign of degeneration as described above (Figure 2A, B). Hydrated eggs may occasionally be present. Elapsed time from spawning <24 h.

Age 1 day: regressing postovulatory follicles, showing degeneration as described for specimens (Figure 2C, D) sampled 24 h after spawning. Elapsed time from spawning ≥24 h but <48 h.

Nonspawning (mature): ovaries with many yolked oocytes; may contain postovulatory follicles in advanced stages of degeneration which cannot be readily distinguished from other atretic structures. Elapsed time from spawning 48 or more hours.

Immature: few or no yolked oocytes.

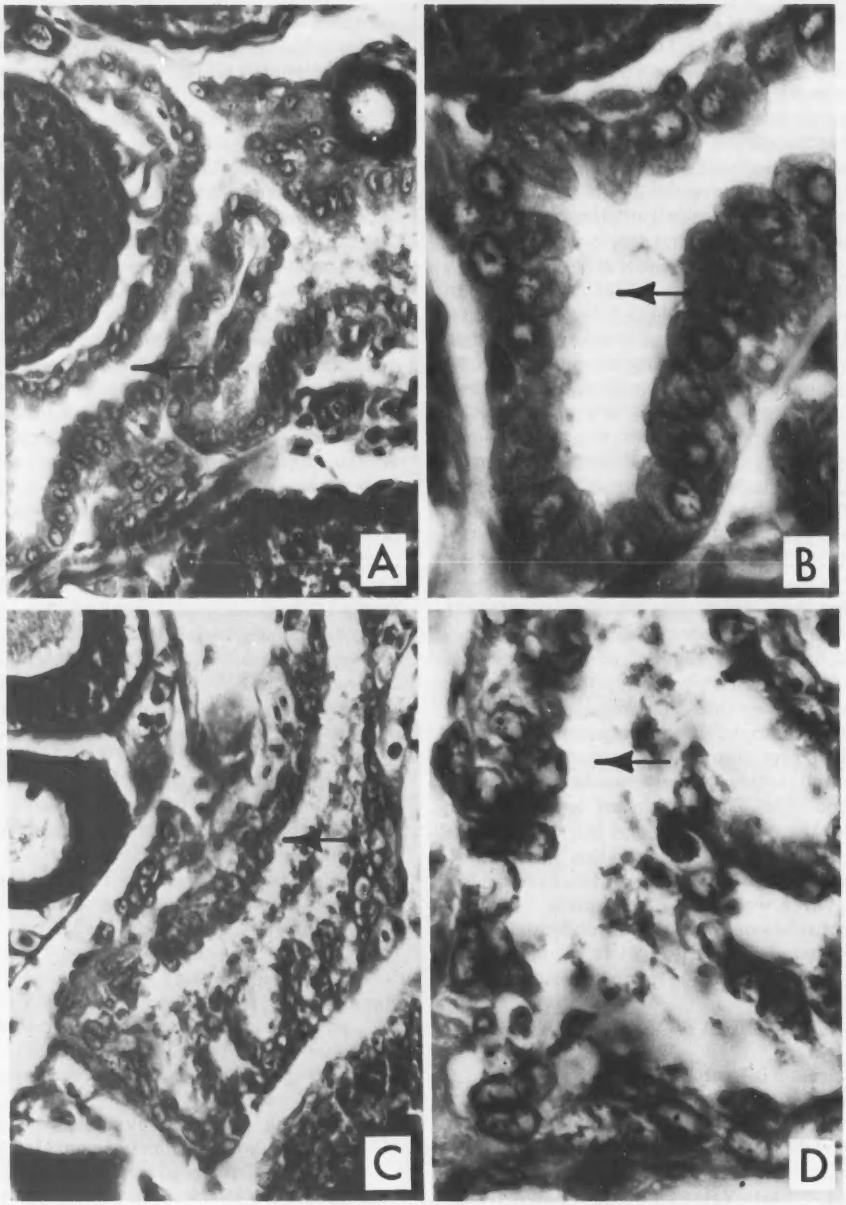

FIGURE 2.—Photomicrographs of northern anchovy ovaries from laboratory specimens: A (400×) and B (1,000×), postovulatory follicles (elapsed time from spawning 0-6 h); C (400×) and D (1,000×), postovulatory follicles (elapsed time from spawning 24 h). Arrow indicates lumen of postovulatory follicle.

TABLE 1.—Results of blind classification[1] (number of females) of postovulatory follicles of female northern anchovy spawned in the laboratory.

Elapsed time from spawning (days)	n	Classification: Postovulatory follicles 0 day	Postovulatory follicles 1 day	Postovulatory follicles older than 2 days or no evidence of spawning	Percent correctly classified
0	21	16	5	0	76
1	19	0	16	3	84
2	23	0	0	23	100
3	20	0	0	20	100
4-9	38	0	0	38	100

[1]Elapsed time from spawning was unknown to classifier.

All sea samples were classed into the above categories. The mean incidence for each category was calculated without regard to the classification uncertainties reported in Table 1. Confidence intervals for mean incidence for each reproductive state were calculated for the February set of samples but not for those taken in March or September because these sets contained only three or four samples. The normal approximation of the binomial distribution was used to estimate the confidence interval (C.I.) for the mean incidence of day 1 postovulatory follicles (95% C.I., Table 2). A normal-log negative binomial distribution (Johnson and Kotz 1970; Zweifel[7]) was used to estimate confidence intervals for the mean incidence of hydrated eggs and new postovulatory follicles because it gave a better fit to the data distribution than did the binomial distribution (Figure 3).

RESULTS

Sexual Maturity

All females taken in February and March were mature, but only 67% of those taken in September were mature. No relation existed between reproductive activity and length in the females examined. Twelve females taken in February in southern inshore stations (Figure 1) were <90 mm standard length (SL), which is smaller than any of

[7]Zweifel, J. R. 1978. Confidence intervals for the mean when sampling from natural environments. Unpubl. manuscr., 10 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 2.—Reproductive state[1] of female northern anchovy collected off southern California in February 1978.

Station number	Day of month	Time of day	Mean length (mm)	Number of females in various reproductive states: Hydrated eggs	Postovulatory follicles 0 day	Postovulatory follicles 1 day	Mature, no evidence of spawning	Total females
2	15	1822	124	0	0	2	9	11
3	15	2053	122	1	2	2	5	10
4	15	2121	116	1	1	1	7	10
5	15	2308	117	2	2	2	4	10
7	16	1908	116	4	0	0	6	10
8	16	2147	106	2	6	0	3	11
9	16	2215	114	0	2	0	8	10
10	16	2326	114	0	1	0	9	10
11	17	0044	112	0	1	1	8	10
13	17	1835	138	0	0	1	10	11
15	17	2132	134	6	0	1	3	10
21	18	2002	137	1	0	0	9	10
27	19	2100	141	0	2	4	4	10
28	19	2230	135	0	1	2	7	10
34	20	2254	138	3	0	3	4	10
37	21	2002	139	0	0	5	5	10
38	21	2117	132	0	0	3	7	10
42	22	1934	103	4	0	3	4	11
45	22	2332	80	0	2	0	8	10
48	23	1838	136	0	0	3	7	10
49	23	2005	122	1	0	1	8	10
50	23	2202	120	0	0	1	9	10
52	24	0125	117	0	0	1	9	10
55	24	1915	126	0	1	3	6	10
57	24	2224	125	2	0	0	9	11
58	25	0009	120	1	2	4	3	10
62	25	1915	116	2	1	1	6	10
72	27	0045	111	0	0	2	8	10
75	27	2112	112	2	0	1	7	10
ΣX				32	24	47	192	295
%				11	8	16	65	100
[2]95% C.I.				6-19	5-14	12-20	—	—

[1]Immature state not included in table because all females were mature.
[2]95% confidence intervals for mean percent of females in each reproductive class.

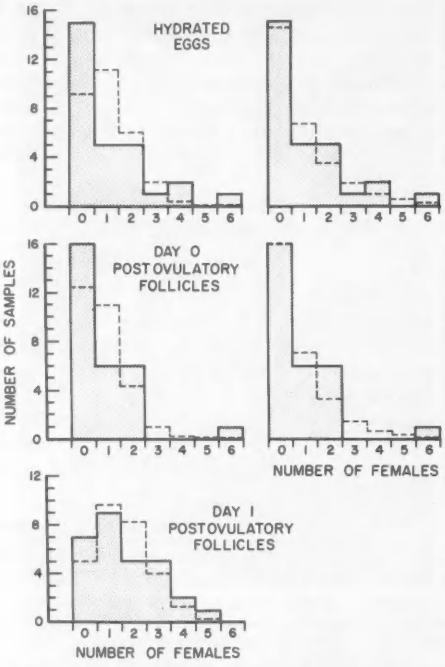

FIGURE 3.—Frequency distribution of the numbers of samples from February 1978 containing 0-6 females in each of three reproductive classes (solid bars). On left sides of the upper two panels are distributions for hydrated eggs and for day 0 postovulatory follicles, compared with that expected (dashed line) from the binomial distribution. On the right sides they are compared with that expected from the negative binomial; the negative binomial gave the better fit in both cases. Bottom panel: the frequency distribution for day 1 postovulatory follicles is compared with that expected (dashed line) from the binomial distribution, which gave an adequate fit to the data.

the reproductively active females found by Clark and Phillips (1952). They reported that only a few females mature at 90-100 mm SL, about 30% mature at 100-120 mm, and 50% at 130 mm, whereas all females we collected in February and March, regardless of size, were sexually mature. Similar to our observations, Brewer (1978) reported anchovy as small as 81 mm SL with well-developed ova from San Pedro Bay. The size of anchovy at first reproduction may have changed since 1946-52 when Clark and Phillips made their observations. On the other hand, all of our collections and those of Brewer (1978) were from southern California whereas those of Clark and Phillips (1952) included collections from the north (Monterey). It is possible that specimens living at the northern end of the range of the central subpopulation could be larger at first maturity.

Incidence of Spawning

Variation existed in the percentage of females occurring in the three reproductive states that were indicative of imminent or recent spawning. Of the females taken in February, 11% had only hydrated eggs, 8% had new postovulatory follicles, and 16% had 1-day-old postovulatory follicles (Table 2). It is critical to our objective of estimating spawning frequency to consider which of these states provided the better estimates. The distribution of the number of samples containing females with hydrated eggs and that for females with 0 day postovulatory follicles gave a poor fit to the binomial distribution indicating possible bias from contagion within samples, whereas no such problem existed for 1-day-old postovulatory follicles (Figure 3). Furthermore, evidence existed for a bias in sampling females with hydrated eggs and those with new postovulatory follicles that was related to time of day (discussed below) and with sexual composition of the school (to be discussed in a separate section). For these reasons, we believe the 1-day-old postovulatory follicles are the preferred estimator of spawning frequency.

Anchovy spawn only at night, and estimates made by Smith[8] from staged eggs indicated that most spawning occurs between 2000 and 0400 h. Since hydration precedes ovulation and spawning, one would expect the females with hydrated eggs to be the most common before 2000. In February, females with new postovulatory follicles were probably undersampled and females with hydrated eggs possibly oversampled, because most samples were taken before midnight. No females with hydrated eggs occurred in the February collections at night before 1900 h; six March females taken in the morning showed the first signs of hydration but the eggs were not sufficiently developed to be classified as hydrated. In February the number of females with hydrated eggs increased sharply after 1900 and generally remained high until 2400 (Table 3). Females with new postovulatory follicles occurred for the first

[8]Smith, P. E. 1978. A field study of anchovy spawning time. Southwest Fish. Cent. Admin. Rep. No. LJ-78-8, 1 p. Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 3.—Percent of female northern anchovy sampled off southern California in February 1978 with hydrated eggs, and postovulatory follicles (age 0 day and age 1 day) by time of day.

Time	Percent of females			Total no. of females
	Hydrated eggs[1]	Postovulatory follicles		
		0 day[2]	1 day	
1801-1900	0	0	19	32
1901-2000	24	5	17	41
2001-2100	6	8	24	50
2101-2200	22	14	12	51
2201-2300	10	6	12	51
2301-2400	7	17	7	30
0001-0100	3	10	23	30
0101-0200	0	0	10	10
Total				295

[1]Only hydrated eggs, no postovulatory follicles.
[2]Includes some females with hydrated eggs and new postovulatory follicles.

time between 1900 and 2000, but were more common later in the night. As expected, the occurrence of females with 1-day-old postovulatory follicles showed no pattern with time of sampling.

Despite our failure to obtain fish over the entire night of spawning, the proportion of females in February with hydrated eggs, combined with those with new postovulatory follicles, was 19% and within the confidence interval for the estimate based on 1-day-old postovulatory follicles (Table 2).

February data indicate that spawning over a 2-wk period occurred at a rate of about 16±4% of the population per night. This means that mature females spawned every 6-7 days. The three purse seine samples taken in March 1977 also indicated a high frequency of spawning; 14% of the females had 1-day-old postovulatory follicles and 9% had new postovulatory follicles (Table 4). The March collections were taken in the early morning after spawning had ended, hence the new and 1-day-old postovulatory follicles can be considered as separate estimates of spawning frequency for different days. This line of reasoning leads to the conclusion that the proportion of females spawning in March may have been about 12%, equivalent to spawning every 8 days.

Of the 24 females taken in September, only 1 had hydrated eggs, 2 had new postovulatory follicles, and none had 1-day-old postovulatory follicles. Lower spawning activity would be expected in September because egg and larval survey data indicate peak spawning usually occurs in February and March and has declined greatly by September although some spawning occurs throughout the year (Lasker and Smith 1977).

Sex Ratio and Incidence of Spawning

The sex ratio of northern anchovy schools is known to vary markedly from schools composed of nearly all females to ones composed of nearly all males (Collins 1969; Klingbeil 1978). It seemed useful to determine if spawning activity varied with sex ratio because the greatest variability in sex ratio occurs during the peak months of spawning (Klingbeil 1978). Twenty-five fish from each trawl sample taken in February 1978 were sexed. We grouped these samples into three classes on the basis of sex ratio (number of females/(males + females)) and calculated the proportion of females in each of the three sex ratio classes that fell within the following reproductive classes: spawning on the night of capture (females with hydrated eggs or new postovulatory follicles); spawning on the night before capture (females with 1-day-old postovulatory follicles); and no evidence of spawning (none of the above categories).

TABLE 4.—Reproductive state of female northern anchovy collected in March 1977 and September 1977 off southern California.

Station number	Day of month	Time of day	Mean SL (mm)	Number of females in various reproductive states					Total females
				Hydrated eggs	Postovulatory follicles		Mature, no evidence of spawning	Immature	
					0 day	1 day			
March 1977									
1	20	0400	120	0	2	11	32	0	45
2	21	0330	119	0	7	6	54	0	67
3	21	0630	113	0	5	4	29	0	38
ΣX				0	14	21	115	0	150
%				0	9	14	78	0	
September 1977									
1	9	2108	124	1	0	0	4	0	5
2	9	2300	129	0	2	0	9	0	11
3	10	2043	113	0	0	0	0	1	1
4	10	2236	112	0	0	0	1	6	7
ΣX				1	2	0	14	7	24
%				4	8	0	58	29	

In samples containing mostly males (mean sex ratio = 0.25), nearly 40% of the females spawned on the night of capture, whereas in samples containing mostly females (mean sex ratio = 0.84), only 10% of the females spawned on the night of capture (Table 5). A chi-square test indicated that the proportion of females spawning on the night of capture differed among the three classes of sex ratios ($P<0.001$) but no difference existed for females with 1-day-old postovulatory follicles. Therefore, most spawning occurred in male dominated schools but females that spawned on the previous night occurred in about equal proportions in all schools.

That groups of pelagic spawners could be male dominated is indicated by the reproductive behavior of another pelagic spawner, the Pacific bonito, *Sarda chiliensis*, described by Magnuson and Prescott (1966). They reported that during courtship, groups of males closely follow a single female. If male anchovy show similar behavior, then trawl collections taken at the time of spawning might be male dominated. To explain the dominance of females in commercial catches, Klingbeil (1978) suggested that male-dominated groups may not form the large dense schools necessary for effective purse seining. It seems reasonable that actively spawning (male-dominated) groups, would not be as likely to preserve the density or the integrity of the school as well as nonspawning groups. Thus, the variability in sex ratio of anchovy schools may be attributable in part to reproductive behavior, that is, the formation of male-dominated spawning groups which may be smaller and less dense than commercial schools. The female component of such groups would be expected to change from day to day because after 24 h, spawned out females occurred with equal frequency in all samples regardless of sex ratio.

Growth of Oocytes

Incidence of postovulatory follicles indicated that in February 16% of the females spawned daily or an individual female spawned on the average once every 6.25 days. In the fecundity section that follows, we show that nearly all of the eggs in the most advanced mode are spawned in one night. Thus, a new mode of eggs must mature every 6-7 days to maintain a spawning frequency of 16%. In the laboratory, spawning begins when the average diameter of the eggs in the most advanced mode is between 0.6 and 0.7 mm. Thus the eggs remaining in the ovary after spawning must attain this size in 6-7 days.

To determine if such rapid oocyte growth seemed reasonable, we estimated the mean diameter of eggs in the most advanced mode and in the second mode for some of the females taken in February and March. Females with hydrated eggs were placed in the same class as those with new postovulatory follicles because hydrated eggs were not included in this analysis. The number of females analyzed and the elapsed time from spawning were: elapsed time 0 day (hydrated eggs and new postovulatory follicles) $n = 43$; elapsed time 1 day (1-day-old postovulatory follicles) $n = 35$; and elapsed time 3.5 days (nonspawning mature females) $n = 38$. The time from spawning in the last class was unknown. We assigned the midpoint of the interval 2-5 days to this class because all fish classified as nonspawning would fall within this interval if the spawning cycle were 6 days. The mean diameter of oocytes in the second mode was estimated only for nonspawning females. In these more mature females, most of the oocytes in the second mode were >0.2 mm, whereas, in less mature fish a significant proportion of the oocytes in the second mode were <0.2 mm, and thus below the lower limit of our measurements.

The average diameter of eggs in the ovary in the most advanced mode immediately after spawning was 0.46 mm; 1 day after spawning it had increased to 0.51 mm and was 0.59 mm in nonspawning females. Figure 4 illustrates how growth in the diameter of eggs in the most advanced mode and

TABLE 5.—Sex ratio in samples (females/(males + females)) and percent of spawning northern anchovy taken in February 1978 off southern California.

Sex ratio			Percent of females			
Sex ratio class	Class mean	Number samples[1]	Spawning on night of capture[2]	Spawned day before capture[3]	No evidence of spawning	Number females classified
0.10-0.39	0.25	7	39	15	46	72
0.40-0.69	0.54	10	16	12	75	101
0.70-0.99	0.84	12	10	20	70	122

[1]Twenty-five fish per sample were used to calculate sex ratio and 10 or 11 females were examined histologically.
[2]Includes females with hydrated eggs and those with recent postovulatory follicles.
[3]Females with 1-day-old postovulatory follicles.

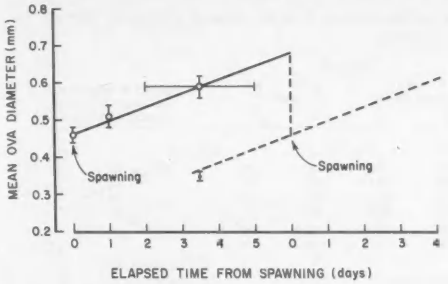

FIGURE 4.—Growth of oocytes in female northern anchovy during an assumed 6-day spawning cycle. Open circles are the mean diameter of eggs in the most advanced mode for: females with hydrated eggs (hydrated eggs excluded) combined with those with recent postovulatory follicles ("spawning"); females with day-old postovulatory follicles (second open circle); and for nonspawning females (third open circle). Horizontal bar indicates period in a 6-day cycle that females would be classified as nonspawning; and the point is plotted at the midpoint of that interval. Vertical bars are ±2 SE of mean and solid circle indicates the mean diameter of eggs in the least advanced mode for the nonspawning class.

that in the second mode could produce a 6-day spawning cycle, the second mode becoming the most advanced mode at the time of spawning. The mean diameter of the eggs in the most advanced and the second mode for the nonspawning class, when plotted at 3.5 days, seems in a reasonable position relative to the other points, indicating that the cycle may be about 6 days. A linear trajectory of oocyte growth of 0.04 mm/day indicates spawning at a diameter between 0.6 and 0.7 mm, in keeping with laboratory findings. This analysis indicates that the mean diameter of yolked oocytes of females in various reproductive stages is consistent with a 6-7 day spawning cycle.

Batch Fecundity

MacGregor (1968) estimated the number of eggs in the most advanced mode in northern anchovy ovaries to be 574 eggs/g wet weight, from an analysis of frequency distribution of eggs in 19 females. Norberg (see footnote 5) concluded that northern anchovy fecundity was 556 eggs/g, from an examination of 119 females. The supposition underlying both estimates was that the number of eggs in the most advanced mode represents the number of eggs spawned. Owing to the importance of batch fecundity in any estimate of spawning biomass from egg and larval production, we decided to reexamine spawning batch fecundity in the northern anchovy.

The assumptions underlying batch fecundity estimates are: all eggs in the most advanced mode are spawned; fecundity is directly proportional to weight; and no bias exists in the estimation of the number of eggs within the most advanced mode nor in the selection of mature females for analysis. We consider these assumptions for females taken in February 1978 using fecundity estimates for each reproductive class.

Histological examination of females with postovulatory follicles indicated that very few hydrated eggs were retained after spawning. Thus, the number of hydrated eggs within ovaries prior to ovulation (females with no postovulatory follicles) should give the most accurate estimate of the number of eggs spawned. Another advantage of using hydrated eggs was that they stand out as an isolated class, distinct from all others; they differ in appearance and are as much as 2-3 times larger than yolked oocytes. Hence, they only need to be counted; neither statistical techniques nor one's judgment need be used to separate overlapping modes.

The mean number of hydrated eggs per gram of female (ovary free) was 389±59 (±2 SE) eggs and was only 7% less than that estimated for females with the most mature ovaries (nonspawner class) (Table 6). Thus, nearly all eggs in the most advanced mode were destined to be hydrated and spawned. Fecundity estimates were substantially higher and more variable in the other three reproductive classes. Many of the females in these classes had only one mode of yolked eggs whereas about 90% of those classified as nonspawners had two modes. Fecundity estimates for the less mature females tend to be higher because the eggs destined to form a second mode have not grown sufficiently to be separated from the rest of the yolked oocytes. More variability exists because of variation among females in the extent of the differentiation of the second modal group of eggs.

In summary, we believe our most accurate estimate of batch fecundity is 389 hydrated eggs/g ovary-free female weight. If an estimate based on total female weight is needed, we recommend the one for nonspawning fish (Table 6) reduced by the fraction of eggs which may not be hydrated (7%). The adjusted fecundity for nonspawners is 368 eggs/g female weight.

Fecundity as estimated above is a function of female weight, ovary weight, and the number of

TABLE 6.—Fecundity (eggs per gram female) estimates for northern anchovy females collected in February 1978 off southern California.

Sample	Number of females	Fecundity: Ovary-free female weight $\bar{x}$	Ovary-free female weight SD	Total female weight $\bar{x}$	Total female weight SD	Percent of females with two modal groups of nonhydrated eggs
Most advanced nonhydrated eggs of females with:						
Hydrated eggs[1]	23	530	360	462	309	39
Day 0, postovulatory follicles[2]	13	693	387	497	201	69
Day 1, postovulatory follicles	19	619	313	592	294	69
None of the above (nonspawners)	33	418	186	396	171	91
Hydrated eggs	23	389	141	340	114	—
MacGregor (1968)	19	606	151	574	131	—

[1]Only the nonhydrated eggs in most advanced mode are included.
[2]Females having both hydrated eggs and postovulatory follicles were included.

advanced eggs in a weighed sample of the gonad. The number of hydrated eggs per gram of ovary did not vary with fish weight and was 2,880±373 (±2 SE) eggs/g of ovary. If any weight-related bias existed, it probably was related to the gonad weight-female weight relation. To ascertain how ovary weight varied with female weight, we separated the data into three classes on the basis of mean diameter of eggs in the most advanced mode and plotted ovary weight as a function of female weight for each class (Figure 5). The relation was slightly curvilinear; the departure from linearity was most ovbious in the 0.51-0.60 mm egg diameter class. Considering the variability in the number of mature eggs per gram of ovary, and the slight departure from linearity, no practical purpose is achieved in expressing fecundity as a function of female weight rather than as a direct proportion of weight, although direct proportionality is somewhat less accurate for extreme weight classes.

The relation between gonad weight and female weight differed somewhat among the diameter classes as can be seen in Figure 5. This might be expected because the weight of the ovary should increase somewhat with the average diameter of the eggs in the most advanced mode. We analyzed the data using multiple regression to determine if the ln (log e) gonad weight (G) could be estimated from the diameter of eggs in the most advanced mode (D), ln ovary-free female weight (W), and the interaction term ($D \ln G$). Both female weight and the interaction term had a significant effect on gonad weight, whereas diameter alone did not. The final multiple regression equation was:

$$\ln G = -4.213 + 1.069 \ln W + 0.555\, D \ln W$$

where $r^2 = 0.92$. Solving for diameter we obtain

$$D = \frac{\ln G + 4.213 - 1.069 \ln W}{0.555 \ln W}.$$

This equation may be useful for estimation of maturity stages for anchovy from weight relationships: 60% of the estimates of mean diameter were within ±0.1 mm of the observed values and the residuals were distributed evenly. The equation is more useful than gonad index (ovary weight/female weight), which is commonly employed to assess maturity, because it produces a number that can be directly related to reproduction and avoids a weight bias for extreme weight classes. The weight bias in gonad index is apparent by examination of data in Figure 5 (lowest); a 30 g female with eggs of 0.65 mm in the most advanced mode has a gonad index of 0.064 whereas that of a 10 g female at the same stage of maturity has an index of 0.040. The equation also identifies females with hydrated eggs; the average diameter of eggs estimated by the equation for females with hydrated eggs was 1.20±0.12 mm (n = 22) and is close to the mean of spawned eggs (1.34 mm). Obviously, such equations would be specific to populations having similar weight relations, but it does seem a useful approach for assessing maturity.

DISCUSSION

This paper provides a method for direct estimation of the frequency of spawning of a multiple spawning pelagic fish population. From such estimates it may be possible to directly estimate spawning biomass from the abundance of eggs and larvae over a short segment of the breeding season. One of the major assumptions underlying the estimate is that a representative sample of females is obtained. Spawning frequency would be overestimated if nonspawning females were in re-

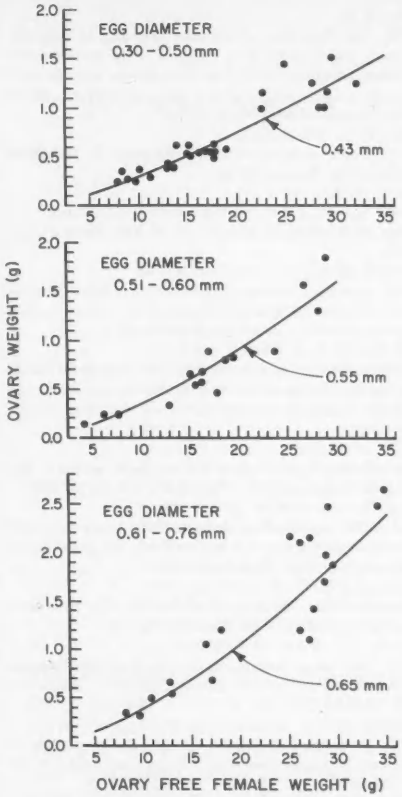

FIGURE 5.—Relation between wet weight of ovary and ovary-free wet weight of female northern anchovy classed into three groups, based on the mean diameter of eggs in the most advanced mode. Each point is a value for a single female. The lines represent multiple regressions, described in the text, for the mean egg diameters given by the arrows.

gions or at depths not sampled by the trawl or commercial purse seine. Studies need to be conducted at other times of the year and employing other sampling techniques to answer these questions.

This paper also describes a new method for estimation of batch fecundity in a multiple spawning fish. Our estimation for northern anchovy based on hydrated eggs (389 eggs/g female weight, less ovary), was substantially less than that of MacGregor (1968) (606 eggs). This difference could be attributed to annual variation in fecundity because variations of this size are known to occur in fishes (Bagenal 1973). On the other hand, our selection of females on the basis of reproductive state also may have been responsible for at least part of the difference. Our estimates for females that had recently spawned (day 0 and day 1 postovulatory follicles, Table 6) were close to MacGregor's estimate. In recently spawned females, modal groups of eggs were less distinct, and often one mode was considered to exist when the eggs may have been destined to form two spawning batches. If MacGregor (1968) used such females, this could explain in part why his estimate was higher than our estimates based on hydrated eggs or on fish classed as nonspawning. In addition, our technique of partitioning eggs occurring between two modal groups according to an assumed normal distribution may have decreased our estimate somewhat relative to past methods. Use of hydrated eggs avoids these problems, but it does require histological examination to insure that none of the females used for the estimate have begun ovulation. Apparently, some of the females we captured were spawning because their ovaries contained many new postovulatory follicles as well as many hydrated eggs. We usually examined only one set of histological sections to determination if ovulation had occurred; histological examination of an entire ovary was impractical. We believe our examination was adequate because our estimate based on hydrated eggs was close to the one based on females with the most advanced ovaries (nonspawning).

In addition to the obvious application to the estimation of spawning biomass, this work provided insights into the reproductive biology of *E. mordax*. The high spawning frequency, the ability to rapidly mature new batches of yolked oocytes, and the long breeding season of the northern anchovy (Lasker and Smith 1977), indicate that energy reserves and the availability of food may set the limit to the number of spawnings and hence to total fecundity. The analysis has also provided a possible explanation for the variability in the sex ratio of catches of anchovy.

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UTILIZATION OF THE NANAIMO RIVER ESTUARY BY JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

M. C. HEALEY[1]

ABSTRACT

Chinook salmon are considered, normally, to spend from a few months to a year rearing in freshwater before migrating to sea. Although large downstream movement of fry, recently emerged from spawning gravels, has been observed in several river systems, it has been suggested that most of these migrant fry are lost to the population. This report describes the fate of downstream migrant chinook salmon fry in the Nanaimo River, British Columbia. In 1975 and 1976 most of the potential fry production from the river system was estimated to have passed by a trapping location near the river mouth. Many of these fry were subsequently found rearing in the intertidal area at the river mouth where salinity was commonly above 20‰. Very few chinook salmon fry were captured at other sampling sites within a 10 km radius of the river mouth. Juvenile chinook salmon were present in the intertidal area of the estuary from March to July each year, but peak numbers occurred in April and May. Peak estuary population was estimated to be 40,000-50,000 in 1975 and 20,000-25,000 in both 1976 and 1977. While in the estuary, chinook salmon grew about 1.32 mm per day or 5.8% of their body weight per day. Individual fish probably spent an average of about 25 days rearing in the estuary and left the estuary when about 70 mm fork length. While in the estuary, juvenile chinook salmon fed on harpacticoid copepods, amphipods, insect larvae, decapod larvae, and mysids. After leaving the estuary, they fed mainly on juvenile herring. The stomach content of chinook salmon captured in the estuary averaged 5% of body weight or less, and varied seasonally and between years. It appears that in the Nanaimo and probably in other systems with well-developed estuaries, that the estuary is an important nursery for chinook salmon fry.

After they emerge from the spawning gravel in early spring, chinook salmon, *Oncorhynchus tshawytscha,* are considered, normally, to spend from a few months to a year in freshwater before migrating to sea (Reimers and Loeffel 1967; Stein et al. 1972; Mehan and Siniff 1962; Lister and Walker 1966). Recently, Reimers (1971) and Dunford (1975) showed that juvenile chinook salmon may also spend considerable time rearing in estuaries after their downstream migration and before moving into high salinity water. Although juvenile chinook salmon are known to occur in a number of British Columbia estuaries (Goodman[2]; Hoos and Vold[3]; Bell and Kallman[4]; Bell and Kallman[5]), the importance of estuarine habitats as nursery areas for young chinook salmon is not well documented. The purpose of this report is to present information on the utilization of the Nanaimo River estuary and adjacent marine areas by juvenile chinook salmon and to consider the importance of the estuary to the stock. Specifically, I shall discuss the timing of downstream movement and abundance of chinook salmon fry in the river; their distribution, abundance, and length of residence in the estuary and in marine waters adjacent to the estuary; and their growth rate and food habits. In this report the term "fry" refers to juvenile chinook salmon that recently emerged from the spawning gravel, often still with externally visible yolk.

METHODS

River Sampling

Downstream migrating chinook salmon fry were captured in seven inclined plane fry traps

[1]Department of Fisheries and Oceans, Resource Services Branch, Pacific Biological Station Nanaimo, B.C., Canada V9R 5K6.

[2]Goodman, D. 1975. A synthesis of the impacts of the proposed expansion of the V.I.A. and other developments on the fisheries resources of the Fraser River estuary. Unpubl. manuscr., 137 p. + append. Environ. Can., Fish. Mar. Serv., Vancouver.

[3]Hoos, L. M., and C. L. Vold. 1975. The Squamish River estuary: Status of environmental knowledge to 1974. Environ. Can., Fish. Mar. Serv. Spec. Estuary Ser. 2, 361 p.

[4]Bell, L. M., and R. J. Kallman. 1976. The Cowichan-Chemainus River estuaries: Status of environmental knowledge to 1975. Environ. Can., Fish. Mar. Serv. Spec. Estuary Ser. 4, 328 p.

[5]Bell, L. M., and R. J. Kallman. 1976. The Nanaimo River estuary: Status of environmental knowledge to 1976. Environ. Can., Fish. Mar. Serv. Spec. Estuary Ser. 5, 298 p.

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anchored in two narrow stream channels near the mouth of the Nanaimo River (Figure 1). (These traps were similar in design to those described by Lister et al. 1969.) The mouth opening of each trap was 30 cm wide by 60 cm deep. Four traps were set side by side in one channel and three in the other. Nylon netting of 5 cm mesh was run between the traps and shore in an attempt to lead additional fry into the traps. The traps were operated in 1975 and 1976 and were set and fished the same way each year. In 1975 the traps were in place from early March to late May, while in 1976 they were in place from early April to late May. Although the main river flow was down a third channel to the west of the traps, a significant fraction of the chinook salmon run passed down the trapping channels and, as will be shown later, the traps captured about 1.5% of the run.

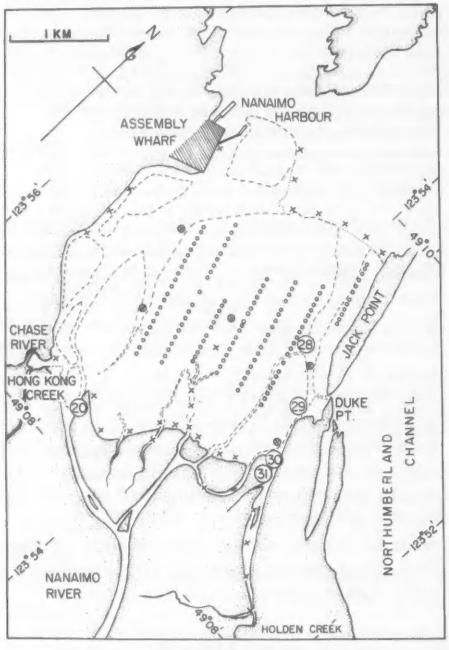

FIGURE 1.—The Nanaimo River estuary. Vancouver Island, showing the location of the fry traps (20) for juvenile chinook salmon; the stations sampled weekly on the east arm of the river and Holden Creek, (28), (29), (30), (31); the general location of seine sets made to determine the distribution of chinook salmon fry in the estuary, ×; and the location of purse seine sets made over the intertidal flats at high tide, ⊗. Small circles show the location of pilings to which log rafts are moored. Most raft storage is on the west side.

Fry captured in the traps between 0800 h of 1 day and 0800 h of the next were counted as a single day's catch. In 1975 the fry were held in live pens in the river and marked a few hours after capture by spraying with fluorescent grit (Healey et al.[6]). After they were sprayed, the fry were held a further 24 h to recover and then were released in the late evening into the river about 2.5 km upstream from the traps. Most mortality from marking occurred in 24 h and was normally <5% (Healey et al.[7]). Each daily catch was examined for marked fry, and total daily run was estimated by mark recapture techniques (Ricker 1975; Healey et al. see footnote 7). In 1976 the fry captured each day were counted and released downstream from the trapping site.

By changing the color of marking grit several times during the run I determined that, on average, 75% of recaptures from a single release were made the night of release, a further 17% on the next night, and the remaining 8% over the next 14 nights. I assumed that these percentages represent the proportions of the marked fry which migrate the night of release or delay migration one or more days. Also, <100% of sprayed fry received a mark. Samples of marked fry examined a few days after spraying showed that usually 95% or more of the fry were marked. The total number of marked fry migrating downstream each night was, therefore, estimated to be the number of fry released, corrected for the proportion unmarked, minus the number expected to delay migration, plus the number expected to be migrating from previous releases. Total daily run was estimated as the product of daily catch and the estimate of marks migrating divided by the number of recaptures. Trap efficiency was the ratio of recaptures to estimated marks migrating.

During about half the trapping days in 1975 no recaptures were made. On these days the run was estimated as the trap catch divided by the overall estimate of trapping efficiency for the year (total recaptures/total marks migrating). Total run in 1976 was estimated from the overall estimate of efficiency for 1975.

[6]Healey, M. C., F. P. Jordan, and R. M. Hungar. 1976. Laboratory and field evaluating of fluorescent grit as a marking material for juvenile salmonids. Fish. Res. Board Can. Manuscr. Rep. 1392, 17 p.

[7]Healey, M. C., R. V. Schmidt, F. P. Jordan, and R. M. Hungar. 1977. Young salmon in the Nanaimo area 1975: 1. Distribution and abundance. Fish. Res. Board Can. Manuscr. Rep. 1369, 161 p.

During April and May 1975, samples of downstream migrant chinook salmon were measured for fork length (millimeters) and wet preserved weight (±0.01 g) to provide an estimate of the body size of downstream migrants.

During 1975 and 1976 the temperature of the river near the trapping site was measured morning and evening. Daily discharge of the river was available from Inland Waters Directorate, Environment Canada, Ottawa. The measurements were made about 12 km upstream from the traps.

Estuary Sampling

In the intertidal area of the estuary most sampling was by beach seine (18 m long × 3 m deep of 12 mm mesh). Stream channels crossing the intertidal mud flat and the delta front were sampled at low tide, and the edges of the tidal marshes at high tide. During March and April 1975 widely scattered locations on the estuary were sampled, but during the latter half of April and May, sampling was concentrated in the east channel of the river and Holden Creek (Figure 1) at low tide. During 1976 and 1977 four specific sampling sites were established in the east channel of the river and Holden Creek and these were fished weekly (Stations 28-31; Figure 1) except that Station 28 was not fished until June 1976, and fishing at Stations 30 and 31 was discontinued after the chinook salmon disappeared from these stations. Sampling at other locations at high and low tide was performed occasionally, as time permitted, to determine the distribution of chinook salmon in the estuary. In addition to beach seining, five sets with a 90 × 7 m hand-hauled purse seine were made over the intertidal mud flat at high tide on 12 May 1976 to determine if juvenile chinook salmon remained over the mud flat at high tide. Catch data are presented as average catch-per-set (CPUE) in this report.

Estuary sampling began during the second or third week of March of each year. In 1975, sampling terminated in early June; in 1976, in mid-July; and in 1977, at the end of June. In 1975, samples of chinook salmon for analysis of length, weight, and stomach contents were preserved in only 6 of 12 sampling weeks. In 1976 and 1977, however samples of 20 or more were preserved each week.

In 1977, temperature (°C) and salinity (per mil) were measured at the time of beach seining at each sampling location in the east channel of the river and Holden Creek with a Yellow Spring Instruments Model 33 Thermister/Salinometer[8].

In 1977 the total population of chinook salmon in the estuary was estimated twice by mark and recapture techniques. Between 18 and 21 April, 3,187 chinook salmon were captured along the east channel of the river and Holden Creek, mainly at Stations 30 and 31, marked with a left pelvic fin clip, and released at the point of capture. Catch and recaptures were recorded on 19-22 April, and on all subsequent sampling days. Between 16 and 19 May, 1,554 chinook salmon captured mainly at Stations 28 and 29 were marked with a right pelvic fin clip. Recaptures of these marks were recorded on 17-19 May, 22 May, and all subsequent sampling days.

Recaptures after the final mark release for each fin clip provided an estimate of the rate of disappearance of marked fish from the sampling area. This rate was assumed constant for each mark and was calculated as the slope of the regression of $\log_e$ (CPUE marks) on days since marking. In calculating the rate for left pelvic clips, catches during the second marking period were ignored since sampling on these days was performed in a way to maximize catch, and was different from our normal sampling procedure. The number of marks released was reduced each day in accordance with these estimated rates of disappearance to give an estimate of the total marks present on each sampling day. Population estimates for each day were, therefore, the product of total catch and estimated marks present divided by recaptures. Left pelvic marks were still present at the time of the second marking, so that it was possible to make two independent estimates of population size at this time.

A sample of chinook salmon was preserved from those captured each day for marking, and these provided an estimate of the average size of marked fish at the time of release. Marked fry captured after the last release of each fin clip were preserved and their fork length and weight measured to provide an estimate of growth rate.

Marine Sampling

Up to 18 different locations within a 10 km radius of the river mouth were sampled in 1975 and 12 locations in 1976 (Figure 2). In 1975 nine

[8]Reference to trade names does not imply endorsement by Fisheries and Oceans, Canada, or by the National Marine Fisheries Service, NOAA.

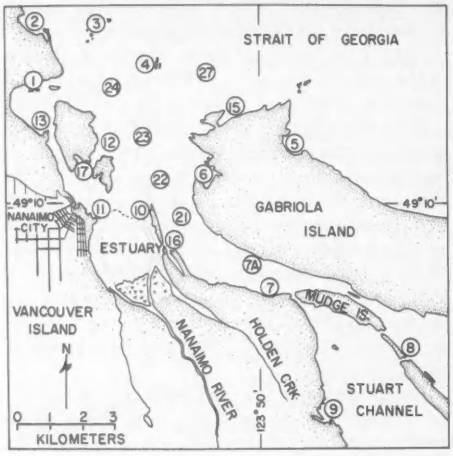

FIGURE 2.—Map of the Nanaimo area, Vancouver Island, showing the locations where beach seine and purse seine sets were made for juvenile chinook salmon (circled numbers).

locations (1, 2, 4, 5, 8, 9, 15, 16, 17; Figure 2) were sampled during the second and third week of May by beach seine (18 × 3 m). Twelve locations (1, 2, 5, 6, 7, 8, 9, 10, 11, 13, 15, 17; Figure 2), were sampled weekly from March to July by hand-hauled purse seine (90 × 7 m). Sixteen locations (1, 2, 3, 4, 5, 6, 7a, 8, 9, 10, 11, 12, 13, 21, 22, 23, 24; Figure 2) were sampled weekly from April to July by drum seine (216 × 18 m), except locations 21-24 which were sampled at 2-wk intervals from late May until early July. In 1976 seven locations (1, 2, 4, 5, 6, 16, 17; Figure 2) were sampled weekly from April to June by beach seine. Ten locations (1, 2, 4, 5, 6, 7a, 10, 23, 24, 27; Figure 2) were sampled by drum seine weekly from early April until the end of July, then approximately monthly until March 1977. In 1977, Area 10 was sampled weekly from late April to late August by the 90 m hand-hauled purse seine.

Sample Processing

Fork length and weight of preserved fish were measured in all years, and in 1976 and 1977, stomach analyses were also performed. The lengths of fish in small catches at sea were occasionally measured at the time of sampling and the fish released. This was especially true of early catches in 1975. In 1977, fish captured by the hand-hauled purse seine in Area 10 were all measured for length, and a subsample of 15-20 was preserved for weight and stomach analyses. Scales of some of the preserved fish from both 1976 and 1977 were examined under 20 × magnification to determine age structure of the catch. Preserved samples were sometimes not analyzed until weeks or months after capture so preserved weights are likely to overestimate live weights. Length, however, is only slightly affected by preservation (Parker 1963).

Wet weights of the stomach contents of individual fish from the intertidal area of the estuary were measured in 1975. Sample size was small except for the 9 May sample (see Table 6). In 1976 and 1977, dry weight of the stomach contents of 10-20 fish from the estuary and a similar sample from off the estuary was recorded each week and converted to percent of body weight by assuming that preserved fish were 20% (average of >20 determinations) dry matter.

Detailed taxonomic analysis of stomach contents was not made. However, in 1976 and 1977 the dominant components of the stomach contents of each sample were recorded.

DESCRIPTION OF STUDY AREA

The Nanaimo River discharges into the Strait of Georgia just south of the City of Nanaimo on the east coast of Vancouver Island (Figure 2). It supports spawning populations of chinook; coho, *O. kisutch;* and chum, *O. keta,* salmon as well as steelhead, *Salmo gairdnerii,* and cutthroat trout, *S. clarki.* Since 1950, chinook salmon escapement has averaged 2,100 spawners, and there has been a gradual decline in abundance from 3,700 spawners between 1950 and 1954 to 1,400 between 1972 and 1976 (Aro[9]; Canada, Fisheries and Marine Service[10]). Adult chinook salmon enter the river between April and October, and spawn from September to November (Aro see footnote 9). In 1974, 1975, and 1976 (the brood years reported in this study) escapement was estimated to be 2,400, 525, and 1,100 respectively.

The delta estuary of the river occupies about 9 km² of which about 6 km² is intertidal mud flat (Figure 1). At the southern margin of the delta the

[9]Aro, K. V. 1973. Salmon and migratory trout of the Nanaimo River and adjacent streams (Revised 1973). Fish. Res. Board Can. Manuscr. Rep. 1284, 15 p.

[10]Annual stream bank estimates of spawning escapement available from Fisheries and Oceans, Canada, Field Services Branch, 1090 West Pender Street, Vancouver, B.C..

river divides into two main channels which cross the intertidal mud flat on the east and west sides. The west channel carries most of the flow, however, and during low river flows in the spring and summer a gravel berm blocks the east channel, probably preventing any fish movement down this channel. Holden Creek flows across the delta on the east side and joins the east channel of the river about half way across the intertidal mud flat. Hong Kong Creek and Chase River enter the delta from the west and join the west channel of the river near the upper margin of the mud flat. The mud flat between the two main channels of the river is dissected by numerous small stream channels fed by seepage from the main river channels. The smaller streams contributing to the delta do not support chinook salmon spawning but do support chum and coho salmon.

Salt marshes at the top of the delta are dominated by black grass, *Juncus gerardii*. The intertidal area has three floral associations: *Fucus-Salicornia* in the upper tidal area, *Ulva-Enteromorpha* in the midtide area, and *Zostera-Ulva* in the low tide area (Foreman[11]). *Zostera* extends in a band across delta front, and well up the east channel of the river.

The intertidal area of the delta is used for log storage by local sawmills and a pulp mill. Part of the northwest corner of the estuary has been filled in during development and expansion of the Port of Nanaimo. Intermittent dredging occurs at the delta front to keep the shipping lane into Nanaimo Harbor open. Some dyking has occurred along the southern margin of the delta to create farm land. Further details of physical and biological features of the estuary and adjacent lands are given in Bell and Kallman (see footnote 5).

Seaward from the intertidal area of the delta a wide variety of habitats provide potential nursery area for juvenile salmon, from sheltered bays and lagoons to exposed rocky or sandy beaches. Many of these habitats were sampled during 1975 and 1976 to estimate the extent of utilization of habitats away from the river mouth as nursery areas (Figure 2). Some details of the physical and biological features of the habitats sampled are given by Healy et al. (see footnote 7). Apart from sampling locations 10, 11, and 17, within the Nanaimo Harbor area (Figure 2), salinity was usually above 27‰, while spring and summer temperature ranged 6°-15° C (Healey et al. see footnote 7).

RESULTS AND DISCUSSION

Downstream Run of Fry

Downstream movement of the chinook salmon fry had two peaks in 1975, the first on 19 April and the second 14 days later (Figure 3). Fry were moving in small numbers throughout March, but most movement occurred in April and May. A total of 10,876 fry entered the traps between 10 March and 24 May.

Trapping began on 8 April 1976, and chinook salmon were already moving downstream. One peak occurred in the 1976 run, although isolated large catches occurred before and after the peak (Figure 3). Only 4,360 fry entered the traps in 1976 suggesting that the total run was about half that in 1975.

Downstream migrants averaged 38.3 mm long (0.57 g) and ranged 33-45 mm long (0.33-1.02 g). Many of the fry still had visible yolk.

River discharge during the the fry run in 1975 ranged 16-100 m^3/s, and increases in fry run were generally associated with increases in discharge.

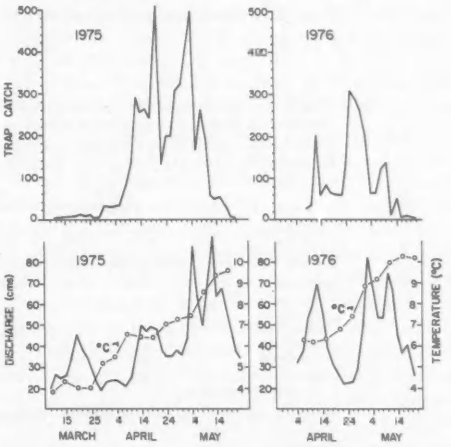

FIGURE 3.—The trap catch of chinook salmon fry (upper panels), river discharge (solid line lower panels), and weekly average river temperature (circles, lower panels) in 1975 and 1976 in the Nanaimo River. Trap catch and discharge are averaged at 2-day intervals for ease of plotting.

[11]Foreman, R. E. 1975. Nanaimo River estuary macrophyte study: Seasonal aspects of macrophyte distribution and standing crop on the Nanaimo River estuary mudflats. BERP Rep. 75-3, final report on Fish. Mar. Serv. Contract OSU4-0217 prepared by R. E. Foreman, Botany Dep., Univ. B.C., 41 p.

Temperature in 1975 ranged 3.1°-11.2° C and was increasing during the run. Greatest fry movement in this year occurred when river temperature was 6°-9° C (Figure 3). In 1976 discharge ranged 18-91m³/s and was higher early in the season than in 1975. Increases in the 1976 fry run often preceeded increases in discharge (Figure 3). River temperature ranged 5.0°-13.3° C and greatest fry movement was when temperature was 8°-11° C (Figure 3).

In addition to temperature and discharge, the catch of chinook salmon in the traps was probably influenced by tide. The traps were set very near the river mouth and at high tide flow past the traps was often negligible. To examine the potential contribution of discharge, river temperature, and tide height to variations in trap catch, I performed a stepwise multiple regression analysis on the data. The dependent variable was trap catch and the independent variables were river discharge, river temperature (morning and evening measurements averaged), average tide height during three periods of the "trapping day" (0800-1800 h, 1800-0000 h, 0000-0800 h), and Julian day of capture. I performed separate analyses on catches preceding and following the peak catch each year. The hypotheses tested were: 1) catch is positively correlated with discharge and temperature and negatively correlated with tide height for all data sets; 2) catch is positively correlated with day of capture prior to peak catch and negatively correlated after peak catch.

The regression analysis failed to confirm or reject either of these hypotheses unequivocally. Discharge was positively correlated with trap catch while catches were increasing, but was not correlated while catches were decreasing (Table 1). Temperature was not significantly correlated with catch in any of the analyses. Tide height was negatively correlated with trap catch while catches were increasing as predicted. While catches were decreasing, however, tide height was uncorrelated with trap catch in 1975 and positively correlated in 1976 (Table 1). The correlation of trap catch with Julian day was positive while catches were increasing and negative while catches were decreasing, as predicted, except that the correlation with increasing catch was not significant in 1976 (Table 1). The multiple correlation coefficients were highly significant and explained 50-79% of the variation in trap catch (R^2, Table 1). Some of the results, like the positive correlations between trap catch and tide height, were counterintuitive, however, and cast doubt on any interpretation of the regression analysis. In spite of these difficulties the regression analysis suggests that discharge and tide height may have influenced trap catch, while temperature probably did not.

Recaptures of marked fry in the traps in 1975 ranged 0-16.6% of the daily estimate of marks migrating. The ratio of recaptures to marks migrating for the whole run was 0.0175, indicating an overall trap efficiency of 1.75% (Table 2).

Peterson estimates of total daily run were made

TABLE 1.—Results of stepwise multiple regression analysis of fry trap catch of juvenile chinook salmon regressed on river discharge, river temperature, average tidal height during three daily time periods (0800-1800 h, 1800-2400 h, 2400-0800 h) and Julian day of capture. Only the regression coefficients for the variables that made a significant ($P<0.05$) contribution to the multiple regression are shown.

Independent variable	Partial Regression coefficient		Standardized partial regression coefficient		Multiple correlation coefficient (R)		R^2	
	1975	1976	1975	1976	1975	1976	1975	1976
Analysis 1: trap catch from first capture to maximum capture: n = 53, 1975; n = 24, 1976								
Discharge	+0.20	+0.40	0.481	0.800				
Temperature	—	—	—	—				
Tidal height:								
0800-1800	—	—	—	—				
1800-2400	—	−15.0	—	0.160				
2400-0800	−78.0	—	0.162	—				
Julian day	+ 6.3	—	0.507	—				
All significant variables					0.873	0.710	0.76	0.51
Analysis 2: trap catch from maximum capture to last capture: n = 22, 1975; n = 31, 1976								
Discharge	—	—	—	—				
Temperature	—	—	—	—				
Tidal height:								
0800-1800	—	+159.8	—	1.77				
1800-2400	—	+122.0	—	1.55				
2400-0800	—	—	—	—				
Julian day	−22.3	−14.2	0.705	1.10				
All significant variables					0.705	0.891	0.50	0.79

TABLE 2.—Trap catch, estimate of marks migrating downstream, recaptures in the traps, and estimated daily run of chinook fry in the Nanaimo River in 1975. Population estimates in italics were derived from trap catch divided by average trap efficiency (0.0175). All other estimates are Peterson type estimates.

Date	Trap catch	Marks migrating	Recaptures	Population estimates	Date	Trap catch	Marks migrating	Recaptures	Population estimates
Mar. 10	2	0	0	*114*	Apr. 17	200	251	3	16,733
11	2	0	0	*114*	18	481	254	8	15,272
12	1	0	0	*57*	19	776	206	10	15,986
13	6	0	0	*342*	20	261	265	21	3,294
14	6	1	0	*342*	21	152	569	9	9,610
15	2	2	0	*114*	22	100	309	4	7,725
16	3	5	0	*171*	23	166	179	0	*9,474*
17	2	3	0	*114*	24	227	116	2	13,166
18	4	3	0	*228*	25	372	162	8	7,533
19	7	2	0	*400*	26	56	120	0	*3,196*
20	11	4	0	*628*	27	425	107	0	*24,255*
21	9	6	1	54	28	190	66	0	*10,844*
22	6	10	0	*342*	29	249	333	2	41,459
23	8	8	0	*457*	30	396	210	2	41,580
24	15	6	0	*856*	May 1	324	233	5	12,582
25	5	8	1	40	2	509	337	5	34,307
26	6	11	0	*342*	3	822	326	2	133,986
27	2	6	0	*114*	4	167	383	6	10,660
28	2	6	0	*114*	5	202	684	19	7,272
29	9	3	0	*514*	6	133	284	4	9,443
30	11	3	0	*628*	7	272	202	5	10,989
31	61	1	0	*3,481*	8	234	144	4	8,424
Apr. 1	14	15	0	*799*	9	497	238	11	10,753
2	49	48	0	*2,797*	10	440	218	6	15,987
3	27	22	0	*1,541*	11	312	409	2	63,804
4	54	39	0	*3 082*	12	104	397	2	20,644
5	36	29	1	1,044	13	48	327	2	7,848
6	57	49	3	931	14	65	150	1	9,750
7	75	37	0	*4,280*	15	51	78	0	*2,911*
8	67	35	0	*3,824*	16	47	60	1	2,820
9	92	64	2	2,944	17	48	59	0	*2,739*
10	173	66	2	5,709	18	66	48	0	*3,767*
11	194	81	0	*11,072*	19	20	45	0	*1,141*
12	381	138	1	52,578	20	14	59	0	*799*
13	293	177	2	25,930	21	5	29	1	145
14	215	311	3	22,288	22	4	18	0	*228*
15	276	288	3	26,496	23	3	6	0	*171*
16	256	210	3	17,920	24	1	6	0	*57*

for 37 days of the 1975 run and ranged 40-133,986 fish/day. The sum of these estimates was 687,568 chinook salmon, and total trap catch for the days when estimates were made was 9,188. The ratio of catch to total run for the Peterson estimates was 0.013, indicating only 1.3% trap efficiency. This estimate was strongly influenced, however, by the large population estimate for 3 May, which resulted from a large catch in which there were few recaptures (Table 2). Ignoring this estimate, the ratio of trap catch to Peterson population estimates was 0.0151, closer to the average efficiency based on mark recaptures.

Population estimates for all days of the run totaled 784,155 in 1975. Assuming trap efficiency was similar in 1976, the run was about 300,000 during the trapping period.

Although most chinook salmon are expected to go to sea after about 2 mo of residence in their natal stream, downstream movement of fry shortly after emergence has been observed in other systems. In the Big Qualicum River, 100 km north of the Nanaimo, between 3,000 and 241,000 fry migrated downstream mainly in March and April from 1961 to 1965, although the time of greatest movement varied from late March to early May (Lister and Walker 1966; Lister and Genoe 1970). The fry migration was followed by a fingerling migration in June which was usually larger than the fry migration. In the Cowichan River, 50 km south of the Nanaimo River, a large downstream movement of fry was recorded during March and April in 1966 and 1967 followed by a smaller fingerling movement in June (Lister et al.[12]). The survival of these fry and their contribution to the adult population were unknown, but presumed to be slight (Lister and Walker 1966).

The number of chinook salmon fry, estimated to have migrated downstream in the Nanaimo River in 1975 and 1976, was 5-10 times greater than in the Big Qualicum River which has a similar escapement (Lister and Walker 1966). This

[12]Lister, D. B., C. E. Walker, and M. A. Giles. 1971. Cowichan River chinook salmon escapement and juvenile production 1965-1967. Can. Dep. Fish. For. Tech. Rep. 1971-3, 48 p.

raises the question: What proportion of the fry population migrates out of the Nanaimo River each year? Information on sex and age of the 1974 and 1975 spawning population in the Nanaimo River is not available so egg deposition can only be surmised. If one assumes, however, that of the 2,400 escapement in 1974, 800-1,000 were females, and that of the 525 spawners in 1975, 200-225 were females, and that the fecundity of Nanaimo River chinook salmon is in the range 6,000-8,000 (Godfrey[13]; Schutz[14]), then potential egg deposition in 1974 was on the order of 6-6.5 million, and in 1975 on the order of 1.2-1.6 million. (The female population was estimated to be <50% of the escapement because of the "jacks.") In the winters of 1974 and 1975 there were no extreme freshets, so survival was probably quite good, perhaps as high as 15-20% (Lister and Walker 1966; Coots[15]). Fry production may be estimated to be, therefore, on the order of 0.9-1.3 million in 1975 and 0.18-0.32 million in 1976. These values are similar to the estimated fry migration each year and indicate that a high proportion of Nanaimo River chinook salmon left the river as recently emerged fry.

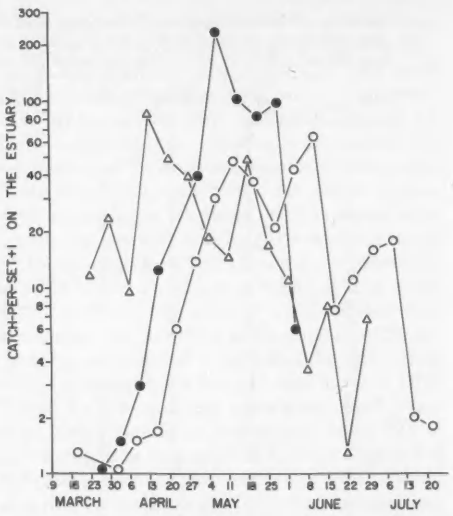

FIGURE 4.—Catch of chinook salmon fry per beach seine set at Stations 28-30 on the Nanaimo River estuary in 1975 (dots), 1976 (circles), and 1977 (triangles).

Distribution and Relative Abundance of Chinook Salmon in the Estuary

Sampling in the intertidal area of the estuary revealed chinook salmon were abundant there in spring and early summer of each year (Figure 4). Juvenile chinook salmon were first captured at the beginning of April 1975, were most abundant in May, and had declined in abundance by early June when sampling terminated (Figure 4). Chinook salmon were captured from mid-March until late July 1976 but increased in abundance later than in 1975, and were generally less than half as abundant as in 1975. Juveniles were already abundant in the estuary when sampling began in late March 1977 and reached maximum abundance in early April, 3 wk earlier than in 1975 and 1976 (Figure 4).

Greatest catches of chinook salmon were in the east channel of the Nanaimo River and Holden Creek. Catches in other stream channels crossing the intertidal mud flat and along the delta front at low tide were small by comparison. Catches in the stream channels in the center of the mud flat averaged only two fish/set, and on the west side of the delta only one chinook salmon was captured in eight sets.

Catches across the delta front at low tide averaged eight fish/set. At the same time catches in the east channnel and Holden Creek averaged 20-40 chinook salmon/set. Catches along the edges of the salt marshes at high tide were lower than in the east channel in 1975, but of similar size in 1977. Purse seine sets over the intertidal flats at high tide, even near locations 29 and 30 where chinook salmon were abundant at low tide, produced no chinook salmon (Figure 1).

Catches at Stations 28-31 in 1976 and 1977 indicated that the area of greatest concentration of juvenile chinook salmon moved seaward along the channel as the season progressed (Table 3). The difference in time of maximum abundance between Station 31 and Station 28 was about 5 wk.

Physical conditions during low tide at the sampling stations along the east channel and Holden

[13]Godfrey, H. 1962. Ages and physical characteristics of maturing chinook salmon of the Nass, Skeena, and Fraser rivers in 1964, 1965 and 1966. Fish. Res. Board Can. Manuscr. Rep. 967, 38 p.

[14]Schutz, D. C. 1975. Rivers Inlet chinook sport fishery, 1971-1974. Environ. Can. Fish. Mar. Serv. Tech. Rep. PAC/T-75-9, 24 p.

[15]Coots, M. 1957. The spawning efficiency of king salmon (*Oncorhynchus tshawytscha*) in Fall Creek, Siskiyou County 1954-55 investigations. Calif. Dep. Fish Game, Inland Fish. Branch, Inland Fish. Adm. Rep. 57-1:1-15.

TABLE 3.—Catch of juvenile chinook salmon per beach seine set at different points along the east channel of the Nanaimo estuary during 1976 and 1977. Station locations are shown in Figure 1.

Sampling week starts	Station 28	29	30	31	Sampling week starts	Station 28	29	30	31
Mar. 21, 1976					Mar. 20, 1977		22.5	5.5	4.0
28					27		16.0	22.0	30.0
Apr. 4		0.0	0.5	1.0	Apr. 3	6.5	7.5	1.5	18.5
11		0.3	0.0	0.5	10	0.5	158.5	76.5	99.5
18		0.5	3.5	8.0	17	12.0	31.4	76.0	58.9
25		20.0	13.0	10.0	24		12.0	79.5	23.0
May 2		2.0	15.5	37.0	May 1	35.0	35.0	7.5	1.5
9		34.5	63.7	31.0	8	20.0	24.0	11.5	0.0
16		64.5	24.0	3.0	15	63.8	47.9	3.5	2.0
23		50.0	9.0	1.0	22	31.0	23.0	7.5	2.0
30		68.0	0.0		29	36.0	0.5	1.5	1.5
June 6	85.7	32.5			June 5	6.0	4.5	0.0	0.0
13	3.0	7.3			12	13.5	0.5		
20	1.5	25.0			19	0.0	1.0	0.0	0.0
27	31.5	5.0			26	11.5	0.0		
July 4	21.5	13.0							
11	2.0	0.0							
18	1.0	0.5							

Creek varied considerably with season in 1977. Temperature ranged 9.5°-26.0° C and salinity 2-24‰ (Table 4). In general, temperature increased at all stations from April through June, but this was strongly influenced by variations in river discharge and weather conditions on the day of sampling. Salinity increased throughout the season, but was also dependent on river discharge and local conditions. Large, local variation in physical conditions was indicated by measurements of temperature and salinity at two locations at Stations 28 and 30 in May and June. At Station 28 a small steam channel joined the main east channel. Temperature of the river above where this stream entered was usually lower, and on one occasion 4.5° C lower, than below the entrance. Salinity above the entrance of this stream channel was sometimes higher and sometimes lower than below the entrance, the greatest observed difference being 6‰ (Table 4). At Station 30, Holden Creek joined the east channel of the river. The river was usually cooler than Holden Creek, although on one occasion it was warmer, and salinity of the river was usually lower than Holden Creek. Temperature and salinity values reported, therefore, should be taken as indications of the kind of conditions in which the fish lived at low tide, with considerable latitude for selection by the fish.

The appearance of juvenile chinook salmon in the intertidal area of the estuary was coincident with the buildup of the downsteam run and the rate of increase in catch on the estuary was similar to the cumulative increase in the number of chinook salmon which had moved downstream. In both 1975 and 1976 the estuary population continued to increase after the peak in the downstream run. These observations indicated that the fry which migrated downstream remained in the estuary for some time.

TABLE 4.—Temperature (° C) and salinity (‰) at sampling locations for juvenile chinook salmon on the Nanaimo estuary during 1977. Station locations are shown in Figure 1.

Sampling week starts	Station 28		Station 29		Station 30		Station 31	
	° C	‰	° C	‰	° C	‰	° C	‰
Apr. 3	12.0	16.0	12.0	14.8	13.0	9.5	12.0	10.5
10	10.5		9.5		15.5		15.3	
17	13.0	20.0	13.6	17.8	12.7	13.0	17.8	11.0
24			11.8	2.0	17.0	10.4	17.2	11.3
May 1	17.0	22.8	15.0	12.8	15.8	14.3	20.0	17.0
8	18.0	20.8	18.2	19.8	21.3	21.6	21.4	20.4
					17.0	18.1		
15	16.7	[1]22.1	16.1	22.2	15.0	[2]19.0	15.4	17.8
	18.2	24.5			14.6	20.0		
22	15.8	[1]20.0	15.2	20.8	15.6	[2]22.2	16.9	18.3
	18.2	24.5			15.1	20.4		
29	13.0	[1]20.0	13.2	21.6	13.3	[2]20.6	13.8	19.1
	13.0	14.0			15.1	20.4		
June 5	19.0	[1]17.5	19.0	20.0	25.1	[2]19.8	26.0	19.4
	23.5	14.0			19.9	18.9		
12	19.0	[1]17.8	18.7	18.2	—	—		
	19.3	17.4			19.9	[2]18.9		
19	21.0	24.6	20.2	24.6	20.5	24.0	24.0	24.0
26	21.0	[1]22.3	19.0	22.0	—	—		
	20.3	23.2			19.9	[2]18.9		

[1]Upper measurement above small tributary, lower below small tributary.
[2]Upper measurement in Holden Creek, lower in main river channel.

At low tide the chinook salmon population in the estuary was clearly concentrated in the east channel of the river and Holden Creek. Some juveniles were found in stream channels crossing the center of the mud flat, and some also found their way down to the delta at low tide. The channels crossing the western side of the mud flat, however, were little used by juveniles.

With the incoming tide the chinook salmon moved to the landward margin of the mud flat and at high tide were found in scattered schools all

across the landward margin of the intertidal area. Apparently no chinook salmon, or very few, remained over the intertidal flats at high tide The redistribution of chinook salmon on each tidal cycle, and their concentration in one of several low tide refuges implied active habitat selection. Active selection of habitats at low tide is further indicated by the seaward movement of the center of the population in the east channel and Holden Creek as the season progressed.

The habitats in which chinook salmon were captured ranged from a few centimeters to a meter or more in water depth, on gravel, sandy, or muddy substrates, with and without eelgrass, *Zostera* sp. In the east river channel, concentrations of fry were found mainly in pools and back eddies. There were, however, no obvious qualitative differences between preferred sites in Holden Creek where chinook salmon were abundant and stream channels crossing the central and west sides of the intertidal area where chinook salmon were scarce. The upstream portions of the stream channels in the central area of the delta, where they cut through the marsh areas, were used as low tide refuges in early spring. Where these stream channels cross the intertidal mud flat deep pools are scarce and the water flow small. These features may have made them unsuitable as refuges during May. The absence of chinook salmon from the west branch of the river could not be explained in this way; however, disturbance of the estuary by log rafting is greatest along the west branch and this may have influenced chinook salmon distribution.

Temperature and salinity in the east channel of the river and Holden Creek indicated that the chinook salmon were tolerating moderate salinities and relatively high temperatures. Occasional measurements of temperature and salinity in other areas sampled at low and high tide were comparable with those in the east channel at low tide. Weisbart (1968) reported that juvenile chinook salmon (parentage not identified) were intolerant of direct transfer from freshwater to 31.8‰ seawater, but that they had greater resistance to seawater than either coho or sockeye salmon, *O. nerka*. McInerney (1964) reported that juvenile chinook salmon from the Samish hatchery, Washington State, avoided all salinites above 0‰ except for a brief preference for about 5‰ salinity in September tests. Presumably both tolerance and preference for salinity will vary among stocks of salmon, and Nanaimo River chinook salmon appear adapted to life in moderate salinity on the estuary. Temperatures experienced by the chinook salmon at low tide were within their tolerance range but were generally above the 12°-13° C reported to be their preferred temperature (Brett 1952).

Seasonal changes in the low tide distribution of chinook salmon were not obviously correlated with temperature and salinity in the east channel and Holden Creek. Temperature at the upstream stations often, though not always, exceeded that at the downstream stations. Chinook salmon were not captured at Stations 30 and 31 when temperature there exceeded 20° C. They were present at Stations 28 and 29, however, when temperature was 20°-21° C. Salinity was only slightly higher on the average at the downstream stations, and often the salinity at the upstream stations was the same or slightly higher than downstream (Table 4). Increasing adaptation to salinity, therefore, appeared not to be a factor in this seaward movement. Possibly the disappearance of chinook salmon from the shallow sampling stations in Holden Creek as the season progressed was an avoidance of the high temperatures that occurred there on sunny days.

The seasonal pattern of abundance of juvenile chinook salmon in the Nanaimo estuary was the same as that observed by Dunford (1975) in the Fraser River, but different from that in the Sixes River, Oreg. (Reimers 1971). In the Sixes River, most chinook salmon apparently spent some weeks in the river before moving into the estuary, although some were considered to have moved directly to the estuary, and some even directly to the sea. Reimers (1971) did not present information on the temperature and salinity of the estuary habitats he sampled. Dunford (1975) gave temperature measurements for two habitat types in the Fraser estuary, and these were lower than in similar areas of the Nanaimo River. Chinook salmon disappeared from Fraser River marsh habitats when temperature reached about 15° C (Dunford 1975).

Size and Growth of Chinook Salmon in the Nanaimo Estuary

Length and weight of chinook salmon captured in the intertidal area of the estuary were only slightly greater than those of downstream migrants throughout the fry run. Toward the end of the fry run, however, average length and weight of chinook salmon captured in the estuary increased rapidly and leveled off at around 70 mm fork

length (FL) and 4.2 g (Figure 5). Chinook salmon captured in 1976 were slightly smaller on the average, than those captured in 1975, while those captured in 1977 were the largest of all. Average size of chinook salmon captured in 1977 increased rapidly 3-4 wk earlier than in 1975 and 1976, in keeping with the apparently earlier downstream run in 1977. The differences in size of chinook salmon captured in the 3 yr were not large, at least early in the sampling, and probably reflected differences in the timing of migration rather than differences in growth rate. The small change in length and weight of chinook salmon in the estuary during March and April probably resulted from continued recruitment of downstream migrant fry to the estuary population, while the increase in May and June reflected growth of the fish residing in the estuary. Seventy millimeters fork length is apparently the size at which chinook salmon leave the estuary and disperse into the marine environment. No young-of-the-year <70 mm were captured away from the estuary. The smallest young-of-the-year captured in area 10 were 70-75 mm FL. Weisbart (1968) commented that 70 mm was about the size at which juvenile chinook salmon became physiologically capable of tolerating high salinity water.

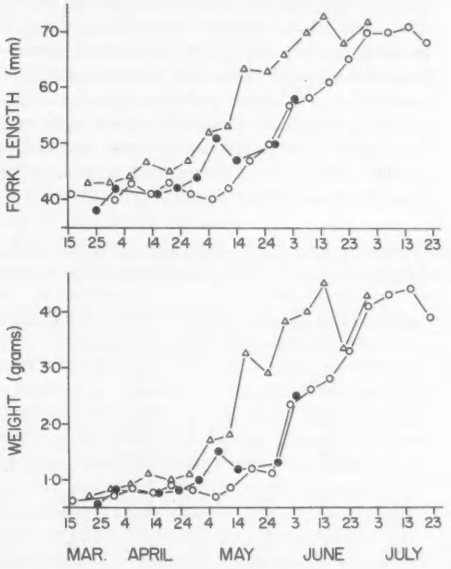

FIGURE 5.—Average fork length and round weight of juvenile chinook salmon captured on the Nanaimo River estuary in 1975 (dots), 1976 (circles), and 1977 (triangles).

The increase in size of chinook salmon on the estuary in June was not representative of their true growth rate, as it was influenced by both the continued immigration of small fish from the river and the emigration of fish reaching 70 mm FL. Recaptured fin clipped fish in 1977, however, provided an estimate of the growth rate of a known group of juveniles. Total mark recaptures sampled for length and weight were 36 left pelvic clips and 19 right pelvic clips. Left pelvic clips averaged 44 mm and 0.92 g when marked, and five of these recovered 47 and 57 days after marking averaged more than 100 mm and 13 g (Table 5). Right pelvic clips averaged 63 mm and 3.36 g when marked, and increased to more than 100 mm and 13 g after 29 days (Table 5). The linear regressions of length or $\log_e$ weight on days since marking indicated no significant difference in the rate of growth between the two marked groups. The data were, therefore, combined by scaling to 0 length and weight at the day of release and growth rates were calculated for the combined data. Growth in length was 1.32 mm/day. Instantaneous daily growth in weight was 0.0566, or about 5.8% of body weight/day.

Estimates of Total Estuary Population

Although the beach seine samples taken in this study provided an adequate measure of distribution and relative abundance of chinook salmon, they do not permit an estimate of the total number of chinook rearing in the estuary. Mark and recapture estimates of abundance in 1977 provided a reference point for comparing catches between years and for comparing the downstream run of fry with the estuary population. Between 18 and 21 April 1977, 3,187 fish marked with a left pelvic clip were released at Stations 29-31 of the east

TABLE 5.—Size at release and recapture of fin-clipped juvenile chinook salmon in the Nanaimo River estuary in 1977.

Left pelvic clips				Right pelvic clips			
n	Days since marking	Average length	Average weight	*n*	Days since marking	Average length	Average weight
55	0	44	0.94	36	0	63	3.36
10	5	47	1.05	12	5	65	3.32
10	13	54	1.90	2	13	71	4.67
1	14	55	1.95	2	19	84	8.29
2	19	60	2.72	1	26	79	5.28
6	26	70	4.60	2	29	107	13.55
2	33	77	5.38				
4	47	103	13.80				
1	57	115	18.60				

channel. Sampling along the east channel and Holden Creek on 22 April showed that the marked fish occurred all along the east channel and Holden Creek but were most concentrated at Station 31 and for several hundred yards farther upstream. Sampling in subsequent weeks indicated that marked fish remained concentrated at Stations 30 and 31 as long as chinook salmon were abundant there. With the shift in population center to Stations 28 and 29, the marked fish also shifted downstream, but remained most abundant at Station 29. A few marked fish were also captured in samples taken across the delta front and across the landward margin of the mud flat at high tide, but none were captured in stream channels in the center of the mud flat at low tide. In spite of their twice daily migration up and down the delta with the tide, therefore, marked fish remained concentrated in the area of marking, so that population estimates from the recaptures referred only to the east channel and Holden Creek, and underestimated the population in this region as well.

The instantaneous rate of disappearance of marks from the sampling area after the April marking was 0.117, or about 11%/day, and after the May marking the rate was 0.137, or about 13%/day. These disappearance rates were used to correct the summed release of marks each day to an estimate of the marks remaining in the area and to calculate estimates of the marked population on all sampling dates following the last release of marks (Table 6).

Estimates of population size throughout the first period of marking were consistent, ranging only 14,675-17,133, and estimates for 25 April and 3 May were also similar (Table 6). On May 9, the population estimate dropped to 5,708 and remained at this level or lower throughout May. The first population estimate from right pelvic clips was on 17 May. Estimates based on this mark ranged 4,629-9,544 between 17 and 19 May and remained at this level throughout May. Estimates for the first 2 wk of June from recaptures of right pelvic clips were 2,352 and 1,204, respectively.

Estimates from right pelvic recaptures in May were twice as great, or greater, than estimates from left pelvic recaptures. Possibly this difference occurred because fishing during 17-19 May was concentrated where fry marked with left pelvic clips were most abundant, so that recaptures of this mark were high.

The estimates indicated that the population in the east channel and Holden Creek was 12,000-19,000 throughout April and early May and that the population declined to 5,000-10,000 in the latter half of May and declined further to about 2,000 in early June. These changes are consistent with changes in beach seine catches.

During the first week of May sampling was performed across the landward edge of the mud flat at high tide (13 sets) in the east arm and Holden Creek (8 sets), across the delta front at low tide (8 sets), and in the stream channels crossing the center of the mud flat (7 sets). Although this sampling was not at random with respect to either the distribution of chinook salmon or marks, it does permit a population estimate based upon sampling areas outside the east channel and Holden Creek. A total of 406 chinook salmon were captured, of which 12 were recaptures. The average

TABLE 6.—Release and recovery of fin-clipped chinook fry, estimates of marks available and population estimates for the Nanaimo River estuary in 1977. LV = left pelvic clip; RV = right pelvic clip. Population estimates are the product of total catch and estimated marks present divided by marks recaptured.

Date	Total catch	Total marks released		Marks recaptured		CPUE recaptures		Estimated marks present			Population estimates		
		LV	RV	LV	RV	LV	RV	LV	RV	Both	LV	RV	Both
Apr. 18	589	370											
19	875	827		18				329			15,993		
20	858	791		55				1,028			16,037		
21	1,344	1,199		127				1,619			17,133		
22	609			104		8.00		2,506			14,675		
25	229			23		3.83		1,764			17,563		
May 3	168			10		1.25		692			11,558		
9	111			2		0.22		343			18,648		
16	233		203	6		0.75		151			5,708		
17	340		335	17	13	1.55	1.18	134	177	311	2,680	4,629	3,525
18	749		691	23	35	2.56	3.89	120	446	566	3,908	9,544	7,309
19	412		325	22	48	2.75	6.00	106	992	1,098	1,985	8,515	6,463
20	127			2	13	0.25	1.62	67	761	828	4,254	8,089	7,010
31	79			0	3	0.00	0.38	26	254	280		6,689	7,373
June 6	21			0	1	0.00	0.12	13	112	125		2,352	2,625
13	28			0	1	0.00	0.25	5	43	49		1,204	1,372
20	2			0	0	0.00	0.00	3	16	19			
28	13			0	0	0.00	0.00	1	5	6			

estimated marked population for the week was 655, giving a population estimate of 22,148 for the whole estuary. The average population of the east channel for the week was about 15,000, or about 68% of this estimate. Total estuary population may, therefore, be about 32% greater than the estimate for the east channel and Holden Creek.

Comparing beach seine catches for 1975-77 with the mark recapture estimates indicated that the peak population on the estuary was on the order of 20,000-25,000 in 1976 and 1977 but was probably closer to 40,000-50,000 in 1975. These estimates are comparable with a single day's fry migration in 1975 and 1976. However, the slow rate of disappearance of marked fry from the east channel indicated a relatively long residence of fry on the estuary (about 60 days). An accumulation of fry on the estuary during downstream migration would, therefore, be expected. Treating each daily run of fry as a single cohort arriving on the estuary, and reducing that cohort by 11-12%/day (the rate of disappearance of marked fry from the east channel), produced estimates for the estuary population of around 100,000 in 1975 and 50,000 in 1976, or about twice the estimate based on mark recapture results for 1977. Estimates of downstream run are for the release point of the marks, however, and significant mortality might occur between the release point and the estuary (Hunter 1959). Alternatively, the rate of disappearance of marked fry may underestimate the rate of disappearance of recent downstream migrants. A disappearance rate of 11-12%/day suggested an average residence time of about 60 days, whereas growth rates suggested that most fry should spend only 25 days in the estuary.

If downstream migrants spend only 25 days in the intertidal area, and their rate of disappearance is constant during that time, then peak estuary populations are 40,000 in 1975 and 20,000 in 1976, comparable with the estimate based on mark recaptures in 1977. The estimate of disappearance rate from mark returns has rather wide confidence limits, 25 days being within the range of 95% probability in estimates of residence time. The apparent discrepancy between mark recapture estimates of estuary population size and downstream run can be resolved by assuming residence of 25 days, therefore. The assumption of a constant rate of disappearance of chinook salmon from the estuary population, however, implies the disappearance of many juveniles <70 mm FL. Although high mortality of salmon fry is a common assumption, no predators or important diseases were obviously present in the Nanaimo estuary to justify the assumption of heavy losses of small fish. The tentative agreement between the various estimates of population size may therefore be spurious, and these estimates should be regarded as preliminary at best.

By comparison with the Fraser and the Sixes Rivers, chinook salmon were rare in the Nanaimo River. Dunford (1975) reported maximum densities in excess of 2 fish/m² in Fraser River marshes, compared with average densities of about 0.1 fish/m² in the east channel and Holden Creek. For the Sixes River estuary, an area about twice as large as the east channel and Holden Creek, Reimers (1971) reported maximum population estimates of 100,000-150,000. However, Reimers' estimates were made 5 days after the release of marked fish into the estuary, and, assuming his marked fish were disappearing at a rate similar to those in the Nanaimo River, the population in the Sixes River estuary may have been closer to half the values he reported. Nevertheless, this still represents a population significantly more dense than that in the Nanaimo estuary. In terms of suitable habitat, however, the Sixes River may not be greatly different from the Nanaimo River, as it is about twice as large as the east channel and Holden Creek, and probably supported about twice the population of chinook salmon.

Population of Juvenile Chinook Salmon Outside the Estuary

Beach seine samples in areas other than the intertidal area of the estuary produced few juvenile chinook salmon. In 1975, 19 sets made in mid-May yielded only 3 juveniles, and in 1976, 61 sets made during April-June yielded only 26. Twenty-four of these were captured in the lagoon behind Duke Point (area 16), adjacent to the estuary. Apparently onshore areas away from the estuary were not used by chinook salmon fry, although all the beaches sampled were used by pink and chum salmon fry.

Juvenile chinook salmon were captured in most locations sampled by the two purse seines in 1975 and 1976. Not all chinook salmon captured were young-of-the-year, however. Catches prior to May were mainly yearlings. In late May and early June there was a large influx of young-of-the-year and a subsequent decline in the catch of yearlings. The influx of young-of-the-year (Figure 6) coincided

with the decline in abundance of chinook salmon in the intertidal area of the Nanaimo estuary. The periodicity of catches in the estuary and adjacent marine areas is indicative of a stage movement away from the estuary and into deeper water by young-of-the-year. Sampling by drum seine after July 1976 indicated the persistence of moderate numbers of juvenile chinook salmon in the Nanaimo area until the end of October, after which catches declined to the low levels observed in spring (Figure 6).

Catches of chinook salmon by the 92 m purse seine in 1975 were mainly in area 10 (338 of 434 chinook salmon captured), with smaller catches in areas 6, 7, 8, and 11 and few elsewhere. Catches by the 218 m drum seine in 1975 were also mainly in area 10 (101 of 205 captured), with the remaining catch scattered throughout the sampling areas. Chinook salmon were more scattered in 1976, area 10 yielding only 79 of 245 captured by drum seine between April and July and areas 1, 2, 5, and 6 also providing good catches. Chinook salmon were of similar abundance in drum seine catches between April and June 1975 and 1976 (CPUE 0.73 in 1975 and 0.83 in 1976) but were significantly less abundant in July 1976 compared with 1975 (CPUE 3.30 in 1975 and 2.28 in 1976 $\chi^2 = 6.43$, $P<0.05$). The greater catch in July 1975 presumably reflected the greater contribution of young-of-the-year from the estuary in 1975.

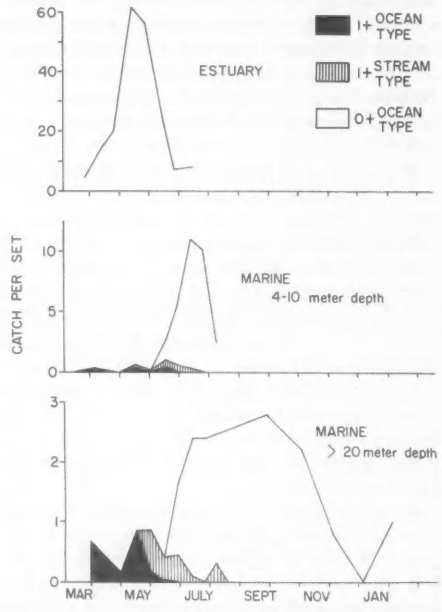

FIGURE 6.—Catch per set of juvenile chinook salmon by age and life history type, by beach seine on the estuary, and by shallow and deep purse seine in marine waters adjacent to the Nanaimo River estuary. Data are averages for 1975-77.

The presence of juvenile chinook salmon in the Nanaimo area throughout the year in 1976 indicates a local resident population that is supplemented by young-of-the-year in June. The appearance of juveniles in large numbers in area 10 coincident with their disappearance from the intertidal area of the estuary indicates that these fish were from the estuary population. The evidence is not conclusive however, and examination of the catch at area 10 in June and July 1977 for fin clips from the estuary produced only 8 marked fish out of 555 examined. This compares with approximately 10% of the estuary population marked in April and May. Possible reasons for the low number of marks in the catch at area 10 include differential mortality of marks (the percentage of mark returns in the estuary declined after each marking), rapid dispersal of chinook salmon away from the estuary, dilution of the fish of local origin by fish from other systems, or dilution of the estuary population by late migrants from the Nanaimo River. In my view the most likely explanations are rapid dispersal of juveniles from the estuary population, and dilution of the estuary population by late migrants from the Nanaimo River. Chinook salmon reared in the intermediate salinity of the estuary are probably already adapted to seawater by the time they are ready to leave the estuary while late migrants from the river might be expected to stay close to the river mouth for some time, adapting to salt water. Samples from area 10 may, therefore, contain a disproportionate number of late migrants.

An unknown proportion of the Nanaimo River population probably disperses rather quickly away from the Nanaimo area after leaving the river. Some young-of-the-year, however, remain in the Nanaimo area, at first concentrated rather close to shore, but later moving to more offshore sampling locations where they persist until at least November (Figure 6). During the winter these fish decline in numbers until by the following spring there are only a few 1+ ocean fish in the local area. Most of these disappear from the surface waters in May coincident with a small influx of yearling smolts from the Nanaimo River (Fig-

ure 6). The yearling smolts dominate samples taken in late May and early June, after which they disappear and are replaced by young-of-the-year, presumably from the Nanaimo River. This sequence of events in which 1+ ocean fish are replaced by 1+ stream fish which in turn are replaced by 0+ ocean fish is not unique to the Nanaimo area but appears to be typical for the Gulf Islands region as a whole (Healey[16]).

Food Habits and Feeding Rates

A growth rate in excess of 5% body weight/day implies good feeding conditions in the estuary (e.g., LeBrasseur 1969). Diets of juvenile chinook salmon were similar in 1976 and 1977, and five taxonomic groups made up the bulk of the diet in the estuary. Harpacticoid copepods were important in March and early April, decapod larvae and amphipods in April and May, and mysids and insect larvae in May-July. Off the intertidal area of the estuary fish larvae, chiefly herring, dominated the diet of juvenile chinook salmon from May through August, while calanoid copepods, decapod larvae, and insects were occasionally important. A shift from a predominantly invertebrate diet to a predominantly fish diet, therefore, occurred as the young chinook salmon dispersed away from the intertidal area of the estuary.

Average weights of stomach contents varied considerably from sample to sample; nevertheless, some generalizations appear possible. Weights of stomach contents of juvenile chinook salmon captured on the estuary in 1975 ranged about 3-5% of body weight in April but dropped rapidly to a low of about 0.1% of body weight as the chinook salmon population on the estuary increased in May (Table 7). Weights of stomach contents of juveniles on the estuary were uniformly low in 1976, never rising above 2.2% of body weight (Table 7). Stomach contents of juveniles captured in 1977 ranged 2-5% of body weight except during the peak of fry abundance when contents dropped to 0.5% of body weight (Table 7). Assuming that stomach contents are a reflection of feeding conditions, it appears that feeding conditions were poorest in 1976, better in 1977, and possibly best of all in 1975 when the population was greatest. Peak population densities were associated with a decline in stomach contents, and by inference, a decline in food intake in the years of good feeding conditions.

TABLE 7.—Stomach contents as a percent of body weight for juvenile chinook salmon captured in the intertidal area of the Nanaimo River estuary and off the intertidal area 1975-77. Sampling week dates are for 1976. Add 2 days for 1975 and subtract 1 day for 1977 to get the correct starting date for those years.

Sampling week starts	On the estuary						Off the estuary			
	1975		1976		1977		1976		1977	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%
Mar. 14			1	1.4						
21					15	1.8				
28			1	1.7	19	3.4				
Apr. 4	9	3.3	2	2.0	24	2.4				
11	3	4.1	6	1.0	20	2.6				
18	1	2.9	20	1.4	57	1.9				
25	5	5.0	20	1.7	15	0.6				
May 2	1	3.8	20	1.6	18	2.0				
9	25	0.1	20	2.2	20	2.2			25	2.6
16	3	2.3	20	1.2	36	4.1				
23			20	1.4	15	2.1				
30			20	1.1	12	4.0	5	2.5		
June 6			20	2.2	10	3.3	1	0.1		
13					6	5.0	13	2.0	14	2.5
20			20	1.9	2	2.0	3	1.3		
27			20	2.0	5	4.0			15	3.4
July 4			20	2.0			3	0.8	17	3.0
11			24	1.8			20	1.2		
18			3	1.0			24	1.3	29	2.7
25							8	1.2	19	1.4
Aug. 15									4	2.3
22									10	1.2

Weights of stomach contents of juvenile chinook salmon captured away from the intertidal area of the estuary were similar to those in the estuary during May and early June, but in mid-June dropped below those from the estuary. Weights of stomach contents of chinook salmon captured offshore were lower in 1976 than in 1977, as was observed for the estuary population (Table 7).

The composition of the diet of juvenile chinook salmon in the Nanaimo estuary was similar to that reported by Sibert and Obrebski (1976) for the Nanaimo estuary in 1973 and to that recorded by Dunford (1975) in similar habitats on the Fraser estuary. The relative timing and importance of specific items in the diet was different than in the Fraser, but this probably reflects differences in abundance of the different diet items and the opportunistic feeding behavior of the fish. The change in diet of juvenile chinook salmon from invertebrates while in the intertidal area of the Nanaimo estuary, to larval fish when away from the intertidal area was consistent with observations on the Fraser estuary. Juveniles in the Fraser River and marsh area fed mainly on invertebrates, but those on Roberts and Sturgeon Banks fed mainly on juvenile herring (Goodman see footnote 2).

[16]Healey, M. C. 1978. The distribution, abundance and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. Fish. Mar. Serv. Tech. Rep. 788, 49 p.

Seasonal changes in the diet of chinook salmon in the intertidal area of the estuary indicated that a combination of size selection and availability influenced the diet. Very small organisms (harpacticoids and cladocerans) occurred in stomachs only in the early spring when the fish were 50 mm or less in length. Larger organisms (amphipods, mysids) were important later in the season when the fish were considerably larger. Insects were important diet items throughout, presumably because of their widespread availability in the habitats sampled.

CONCLUSIONS

The Nanaimo River population of juvenile chinook salmon is composed of fish which go to sea in their first year and fish which remain in freshwater for 1 yr, with those which go to sea in their first year most numerous. Chinook salmon which migrate to sea in their first year are the most common life history type in British Columbia (Milne[17]; Godfrey see footnote 13). In the Nanaimo River many of those chinook salmon which go to sea as young-of-the-year move downstream as recently emerged fry and rear to smolt size in the intermediate salinity of the estuary. Large numbers of chinook salmon fry are found in the marshes of the Fraser estuary in spring and summer (Dunford 1975) and in the estuaries of other rivers in which chinook salmon spawn (Healey unpubl. data). Estuaries, therefore, are important nursery areas for chinook salmon, a fact which has not hitherto been appreciated.

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COMPOSITION, ABUNDANCE, AND DISTRIBUTION OF ZOOPLANKTON IN THE NEW YORK BIGHT, SEPTEMBER 1974-SEPTEMBER 1975

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ABSTRACT

Zooplankton taxa were counted in 8 to 19 samples from each of 11 cruises in the New York Bight between September 1974 and September 1975. Major seasonal events were an influx into the region of tropical-subtropical copepod species during autumn 1974 and summer 1975, an offshore (>50 m water depth) zooplankton abundance maximum in March dominated by the pteropod *Limacina retroversa*, a second offshore maximum in May characterized by high abundance of the copepods *Pseudocalanus* sp., *Calanus finmarchicus*, and *Oithona similis*, and an onshore (<50 m water depth) maximum in July characterized by high abundance of the copepods *Centropages typicus* and *Temora longicornis*. The offshore maxima occurred during or shortly after the local spring phytoplankton bloom (March-April). Advection of pteropod and copepod stocks into the region from the northeast probably contributed to these peaks. The July *C. typicus-T. longicornis* peak was associated with summer warming of the water column within the highly productive waters in the Bight apex and off the New Jersey coast. Comparison of our results with those of a study conducted in 1959-60 shows that the most abundant species of copepods were essentially the same during the two periods.

The New York Bight is the section of continental margin and overlying water within the bend of the Atlantic coastline bounded by Long Island on the north and New Jersey on the west (Figure 1). It is one of the most heavily used coastal regions of the world for a variety of human activities, including transportation, fisheries, recreation, and waste disposal (Gross et al. 1976). Exploration for and exploitation of potential offshore petroleum deposits may place additional burdens on the region's environment. Efforts to document changes in the biota because of these activities have generally been inadequate, especially in regards to the zooplankton. In a recent review, Malone (1977) observed that studies of the zooplankton of the New York Bight generally have been restricted to small geographic areas and to short periods of time, and consequently little data on species abundance and distribution exist for most of this heavily exploited area.

In this paper, we examine seasonal and onshore-offshore trends in occurrence and abundance of zooplankton taxa in waters of the New York Bight. These observations are based on analysis of the most comprehensive set of zooplankton samples obtained to date within the region and thus are invaluable for comparison with future studies. We compare our results with previous studies for evidence of the year-to-year variations in mean abundance of dominant species and in timing of peaks in their standing stocks. Finally, we examine occurrences of offshore water within the study area, and discuss zooplankton abundance maxima in relation to seasonal and regional variations in temperature and phytoplankton standing stocks and the environmental requirements of the dominant species.

METHODS

The station grid (Figure 1) was occupied 13 times between 25 July 1974 and 15 September 1975, with a cruise every month except December 1974 and January 1975. These cruises were part of an ichthyoplankton survey by the National Marine Fisheries Service (NMFS) Laboratory at Sandy Hook, N.J., funded by the Brookhaven National Laboratory. Zooplankton were analyzed in collections from the 11 cruises between 24 September 1974 and 15 September 1975 (Table 1).

Standard NMFS MARMAP gear was used that consisted of 60 cm diameter paired 333 μm and 505 μm mesh nets mounted on a "bongo" sampler without an opening-closing mechanism. Sampling accessories (flowmeters, depth recorder, depressor, towing cable) were rigged as specified by Smith and Richardson (1977). To obtain better estimates of small-bodied copepods, nets with 253

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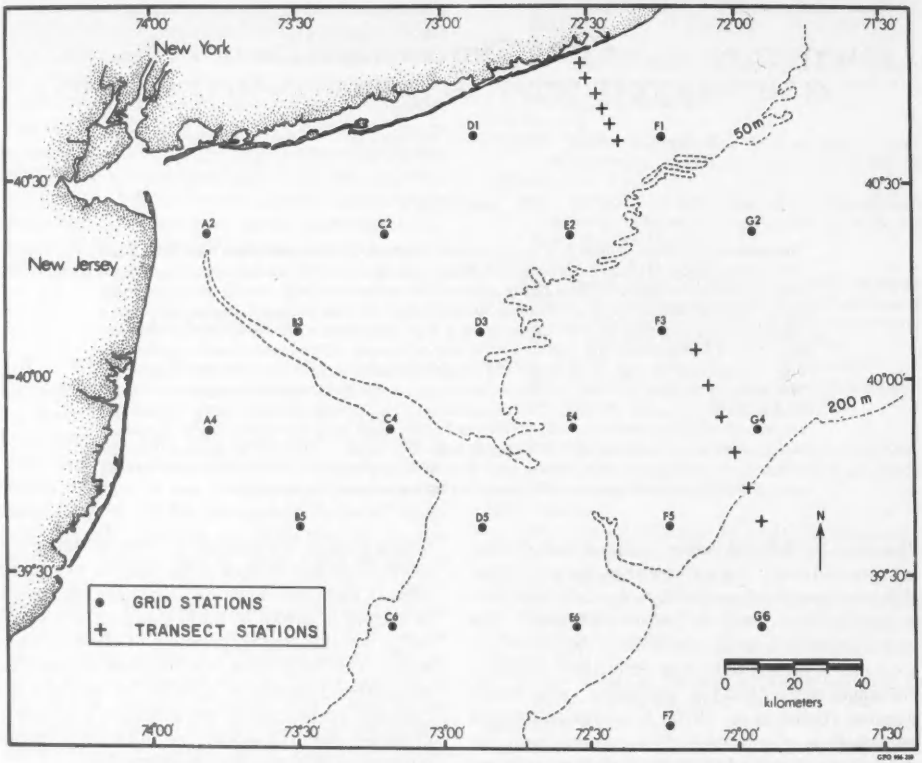


FIGURE 1.—New York Bight with stations for oblique net tows for zooplankton (grid) and chlorophyll, nutrient, and hydrographic measurements (grid and transect).

or 223 μm mesh were added to the sampling array in 1975. These nets were 20 cm in diameter and mounted as pairs on a bongo sampler rigged with a flowmeter in one mouth. The 20 cm sampler was attached to the towing wire immediately above the 60 cm frame, and the entire array was towed obliquely at 3.5 kn (6.5 km/h) from near bottom to surface, except at stations exceeding 200 m where tows were from 200 m to the surface. The samples from the two nets on the 20 cm frame were combined before preservation.

From 8 to 19 of the 20 grid stations (Figure 1) were sampled for zooplankton during the 11 cruises of the survey (Table 1). Samples were not available for every station because of gear failure, adverse weather, or contamination by algae or sediments. At all grid and transect stations (Figure 1) XBT's and nonmetallic sampling bottles were used to obtain temperature, salinity, nutrient, and chlorophyll data at discrete depths.

Samples were analyzed separately for chaetognaths, copepods, and "other" zooplankton (i.e., all taxa other than chaetognaths and copepods). We used only samples from 253 μm and 223 μm mesh nets to estimate the abundance of copepods and other zooplankton in 1975 but had to rely on 333 μm mesh nets for abundance estimates in 1974. In the separate analyses of copepods and other zooplankton, we removed aliquots from a sample with a piston pipette until a total of 500 or more individuals were identified and counted. We counted chaetognaths only in collections from 333 μm mesh nets , which retained most size classes of these large-bodied animals. We used a Folson plankton splitter to subsample collections with large numbers of chaetognaths until a total of 200

TABLE 1.—Zooplankton sampling data for the New York Bight region, 1974-75. Net mesh aperatures and mouth diameters indicated by letters: A, 333 μm, 60 cm; B, 253 μm (February 1975 only) or 223 μm, 20 cm. For station locations see Figure 1.

Station	Depth[1] (m)	Cruise 74-11 24-28 Sept.	74-13 23-28 Oct.	74-15 19-23 Nov.	75-1 1-6 Feb.	75-3 5-11 Mar.	75-4 2-10 Apr.	75-5 6-12 May	75-6 2-9 June	75-7 7-12 July	75-8 12-16 Aug.	75-14 8-15 Sept.
A2	27	A	A	—	A, B	A	A, B	A, B	A, B	A, B	A, B	B
A4	26	A	A	—	A, B	B	A, B	A, B	A, B	B	A, B	A, B
B3	40	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
B5	37	A	A	—	—	A, B	A, B	A, B	A, B	A, B	B	A, B
C2	33	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
C4	49	A	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B
C8	59	—	A	—	—	B	A, B	A, B	A, B	A	A, B	A, B
D1	29	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
D3	49	A	A	A	A, B	A	A, B	A, B	A, B	A, B	—	A, B
D5	64	A	A	—	A, B	A, B	A	A, B	A, B	A, B	A, B	A, B
E2	48	A	—	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
E4	66	A	A	A	A, B	A, B	A, B	A, B	B	A, B	A, B	A, B
E6	124	A	A	—	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
F1	49	A	A	A	A	A, B	A, B	A, B	A, B	A, B	A, B	A, B
F3	71	A	A	—	A, B	A, B	—	A, B	A, B	A, B	A, B	A, B
F5	128	—	A	—	A, B	A, B	B	A, B	A, B	A, B	A, B	A, B
F7	2,800	A	A	—	A, B	A, B	A, B	A, B	A, B	A, B	A, B	A, B
G2	71	A	A	—	A, B	A, B	—	A, B	A, B	A, B	A, B	A, B
G4	146	A	A	—	A, B	—	A, B	A, B	A, B	—	A, B	A, B
G6	1,600	—	—	—	—	—	—	—	—	B	A, B	—

[1]Maximum sample depth = 200 m.

or more individuals were counted. Abundances of taxa within individual samples and related data are available in a data report (Judkins[3]) and from the senior author. In our treatment of the cross-shelf distribution of zooplankton, we divided the study region into two sectors of equal area, an onshore zone shoreward of the 50 m depth contour and an offshore zone seaward of that contour. Each sector contained 10 zooplankton grid stations (Figure 1). This division yielded approximately equal numbers of onshore and offshore samples and provided an easy test for cross-shelf differences in species abundances.

In Tables 2 and 3, we list abundances as both concentrations (numbers/cubic meter) and standing stocks (numbers/square meter). We calculated concentrations primarily for comparison with the historical data which have been reported almost exclusively in that manner. However, it would be an error to compare concentrations from different locations in the New York Bight because of the wide range of depths of stations and the vertical stratification of zooplankton. Estimates of numbers/cubic meter from oblique tows are average values for the entire water column, and these would be adequate for comparisons of tows from different depths only if zooplankton were evenly distributed throughout the water column. However, if a species is restricted to a narrow depth stratum, then its concentration would be underestimated by deeper tows relative to shallower ones (Peterson and Miller 1977). Vertically discrete samples show that most species in the New York Bight are concentrated in the upper 20 to 30 m (Judkins unpubl. data). To avoid underestimating species abundances in samples that extended below about 30 m, we calculated standing stocks and were then able to obtain mean values for combinations of tows from different depths and to test for significant differences between these means.

[3]Judkins, D. C. Zooplankton sampling program and data. *In* E. Wold (editor), Atlantic coastal experiment survey cruises (July 1974-September 1975) data report Vol. 2. Zooplankton and ichthyoplankton, p. 2-129. BNL 24771. Brookhaven National Laboratory, Upton, N.Y.

RESULTS

Frequency of Occurrence of Zooplankton Taxa

We identified 88 copepod species, 10 chaetognath species, and 26 other holo- and meroplanktonic taxa (Table 4). By season, 100 taxa occurred in samples taken in autumn (September-November) 1974, 68 in samples from winter to spring (February-May) 1975, and 91 in samples from summer (June-September) 1975.

These taxa can be grouped on the basis of seasonal and cross-shelf patterns in occurrence. The taxa in one group occurred commonly during all seasons and included the copepods *Centropages typicus*, *Pseudocalanus* sp., *Calanus finmarchicus*, *Paracalanus parvus*, *Oithona atlantica*, *Metridia lucens*, and *Clausocalanus pergens*, the chaetognaths *Sagitta elegans* and *S. serratodentata*, and pteropods, appendicularians, medusae, polychaete larvae, bivalve veligers, and euphausiid furcilia and calyptopsis stages (Table 4). The copepod *O. similis* was uncommon only during au-

TABLE 2.—Mean abundance (no. /m², no. /m³, and percent total no. /m²), frequency of occurrence (% of samples), average rank, and dominance of the 20 most abundant zooplankton taxa in the New York Bight, September 1974-September 1975. Taxa ranked within each sample on basis of number per square meter (1 = most abundant, ties averaged); ranks for each taxon averaged over all samples (n = 178 for chaetognaths, n = 183 for copepods and others). Dominance: proportion of samples in which taxon was among those making up 50% of the individuals; summation in each sample was begun with the most abundant species (Fager and McGowan 1963).

Taxa	Abundance			Frequency	Average rank	Dominance
	no./m²	no./m³	% total	%		
Pseudocalanus sp.	25,566	521	13.8	91	15.7	56
Pteropods	25,532	479	13.8	98	11.7	42
Centropages typicus	25,135	655	13.6	97	8.9	57
Paracalanus parvus	15,342	312	8.3	79	28.2	49
Penilia avirostris	14,613	454	7.9	28	82.9	15
Temora longicornis	11,365	373	6.2	61	50.8	11
Calanus finmarchicus	11,245	146	6.1	91	17.3	36
Oithona similis	8,293	146	4.5	81	28.7	9
Appendicularians	7,076	126	3.8	84	27.2	14
Gastropod veligers	4,833	113	2.6	61	52.3	5
Evadne spp.	3,901	91	2.1	45	65.9	9
Doliolids	3,600	90	2.0	32	79.5	6
Metridia lucens	2,498	21	1.4	58	52.4	8
Plutei	2,239	51	1.2	31	80.5	5
O. atlantica	1,979	22	1.1	72	36.7	17
Clausocalanus pergens	1,821	16	1.0	51	59.4	8
Medusae	1,419	27	0.8	74	40.7	0
Acartia tonsa	1,345	43	0.7	24	85.8	0
Sagitta elegans	1,311	26	0.7	96	30.9	3
Polychaete larvae	926	20	0.5	84	33.6	0
Total copepods	114,383	2,406	62.0			
Total chaetognaths	2,222	43	1.2			
Total "others"	67,769	1,511	36.8			
Grand total	184,174	3,960				

tumn 1974, and that may have been due simply to escapement of this small-bodied species through the coarse-mesh (333 μm) net used then. *Metridia lucens, C. pergens,* and euphausiid calyptopsis and furcilia stages were generally common only offshore, but all others in this group tended to be common throughout the Bight.

A number of taxa were common only during portions of the year. The oceanic copepod *Calocalanus tenuis,* cladocerans of the genus *Evadne,* hyperiid amphipods, and doliolids were common in autumn 1974 and again in summer 1975 but were uncommon during the intervening winter-spring period (Table 4). The neretic copepod *Temora longicornis,* ectoproct larvae, and copepod nauplii occurred commonly during autumn 1974 and winter-spring 1975 but were uncommon during summer 1975. The cold-water oceanic copepod *Pleuromamma borealis* occurred commonly only during the winter-spring period and then only offshore. Another oceanic copepod characteristic of warmer waters, *Mecynocera clausi,* was common offshore during winter-spring and summer 1975. Gastropod veligers were common both onshore and offshore during 1975 but were uncommon throughout the Bight in 1974. A large group of taxa were common only during autumn 1974. This assemblage consisted of copepods *Candacia armata, Oncaea venusta, Acartia tonsa, A. danae, Nannocalanus minor, Centropages bradyi, Rhincalanus nasutus, Eucalanus sewelli, Paracalanus aculeatus, Clausocalanus furcatus, C. jobei, Corycaeus clausi, C. speciosus, Temora stylifera, Scolecithrix danae,* and *Oithona plumifera,* the chaetognath *Sagitta enflata,* the cladoceran *Penilia avirostris,* echinoderm plutei, and siphonophores (Table 4). With the exception of the coastal-estuarine species *A. tonsa* and *P. avirostris* (and probably most of the plutei), members of this group typically inhabit the slope region and adjoining warm oceanic waters (Grice and Hart 1962; Owre and Foyo 1967; Bowman 1971).

The majority of copepods (61) and chaetognaths (7) were uncommon or rare in our samples, and most of these (43) were recorded most frequently or exclusively in autumn 1974 and/or summer 1975. Some of these rare and uncommon species are coastal-estuarine forms (e.g., *Centropages hamatus, Acartia longiremis, A. hudsonica, Paracalanus crassirostris, Tortanus discaudatus, Labidocera aestiva, Anomalocera opalus, Sagitta hispida)* and a few inhabit boreal offshore waters (e.g., *Calanus helgolandicus, Heterorhabdus norvegicus),* but the majority typically have

TABLE 3.—Seasonal variations in mean abundance (no./m² and no./m³) and frequency of occurrence (% of samples) of the 20 most abundant zooplankton taxa in the New York Bight, 1974-75. Values in parentheses are percents of total zooplankton (no./m²) during periods. Asterisks indicate significant differences in mean no./m² between periods (* = $P<0.05$, ** = $P<0.01$, NS = not significant, NT = not tested because of different mesh aperatures of nets used in 1974 and 1975).

		1974		1975			
No. samples (chaetognaths)		Sept. 17	Oct.-Nov. 26	Feb.-Mar. 32	Apr.-May 35	June-July 34	Aug.-Sept. 34
No. samples (copepods, others)		17	26	30	35	37	38
Taxa	Item						
Pseudocalanus sp.	No./m²	1,692 (1.0) NS	507(1.0) NT	116,340 (8.5)**	64,184 (24.1)*	40,855 (18.0)**	9,981 (6.3)
	No./m³	33	11	374	1,163	900	245
	% frequency	71	69	97	100	100	95
Pteropods	No./m²	712 (0.4)**	308 (0.6) NT	81,837 (42.4) NS	43,100 (16.2)**	12,553 (5.6)NS	5,801 (3.7)
	No./m³	13	8	1,215	937	335	149
	% frequency	100	100	100	100	95	97
Centropages typicus	No./m²	16,818 (9.7) NS	19,838 (40.6) NT	30,077 (15.6) **	8,702 (3.3)*	50,801(22.4)NS	18,143 (11.6)
	No./m³	445	606	700	104	1,498	451
	% frequency	100	92	100	97	97	97
Paracalanus parvus	No./m²	2,834 (1.6) NS	6,168 (12.6) NT	17,388 (9.0) NS	5,402 (2.0) NS	13,820 (6.1)**	36,395 (23.2)
	No./m³	74	188	299	41	295	784
	% frequency	94	96	90	31	73	100
Penilia avirostris	No./m²	74,658 (43.0)*	794 (1.6) NT	<1(<0.1) NS	— NS	—*	36,434 (23.2)
	No./m³	2,278	24	<1	—	—	1,152
	% frequency	94	35	3	—	—	63
Temora longicornis	No./m²	139 (0.1) NS	246 (0.5) NT	855 (0.4)**	6,875 (2.6)*	48,173 (21.3)**	529 (0.3)
	No./m³	3	5	30	204	1,605	16
	% frequency	53	62	53	80	84	29
Calanus finmarchicus	No./m²	4,031 (2.3) NS	1,895 (3.9) NT	824 (0.4) NS	26,651 (9.8) NS	16,640 (7.3) NS	9,636 (6.1)
	No./m³	70	32	12	261	231	173
	% frequency	76	81	90	100	95	92
Oithona similis	No./m²	128 (0.1)*	34 (0.1) NT	11,199 (5.8) NS	18,947 (7.1)*	9,836 (4.3)**	3,739 (2.4)
	No./m³	3	<1	221	255	227	68
	% frequency	53	31	83	100	97	95
Appendicularians	No./m²	4,293 (2.5)*	586 (1.1) NT	11,894 (6.2) NS	19,205 (7.2)**	3,136 (1.4) NS	1,623 (1.0)
	No./m³	115	6	204	316	60	39
	% frequency	100	62	60	100	89	92
Gastropod veligers	No./m²	1(<0.1) NS	2(<0.1)NT	6,848 (3.5) NS	13,674 (5.1) NS	5,253 (2.3) NS	159 (0.7)
	No./m³	<1	<1	431	324	149	2
	% frequency	12	4	100	97	70	47
Evadne spp.	No./m²	3,846 (2.2)*	72 (0.1) NT	—**	13,116 (4.9)*	3,884 (1.7) NS	1,156 (0.7)
	No./m³	127	2	—	306	77	23
	% frequency	76	35	—	69	68	34
Doliolids	No./m²	22,022 (12.7)**	65 (0.1) NT	— NS	— NS	389 (0.1) NS	6,191 (4.0)
	No./m³	552	1	—	—	4	183
	% frequency	100	58	—	—	30	39
Metridia lucens	No./m²	221 (0.1) NS	247 (9.5) NT	1,533 (0.8)*	8,195 (3.1)*	1,683 (0.7) NS	1,327 (0.8)
	No./m³	2	4	23	58	15	12
	% frequency	32	62	70	69	47	58
Plutei	No./m²	14,682 (8.5) NS	2,745 (5.6) NT	— NS	1,635 (0.6) NS	48 (<0.1) NS	784 (0.5)
	No./m³	308	90	—	22	1	25
	% frequency	59	54	—	54	14	21
O. atlantica	No./m²	1,354 (0.8) NS	1,742 (3.6) NT	1,498 (0.8) NS	2,350 (0.8) NS	1,963 (0.8) NS	2,497 (1.6)
	No./m³	18	31	27	18	14	24
	% frequency	88	88	100	57	41	76
Clausocalanus pergens	No./m²	142 (0.1) NS	81 (0.2) NT	1,494 (0.8) NS	3,740 (1.4) NS	1,304 (1.4) NS	2,807 (1.8)
	No./m³	1	1	21	27	15	21
	% frequency	41	50	80	29	43	63
Medusae	No./m²	128 (0.1) NS	540 (1.1) NT	511 (0.3)**	4,411 (1.7)*	1,927 (0.9)**	63 (<0.1)
	No./m³	4	16	10	87	33	2
	% frequency	65	85	70	97	78	50
Acartia tonsa	No./m²	4,195 (2.4) NS	435 (0.9) NT	— NS	41(<0.1) NS	—	4,264(2.7)
	No./m³	140	14	—	<1	—	132
	% frequency	71	58	—	6	—	39
Sagitta elegans	No./m²	1,006 (0.6) NS	277 (0.6) NS	478(0.2)**	1,581 (0.6)**	2,850 (1.3)**	1,220 (0.8)
	No./m³	19	5	9	55	61	19
	% frequency	100	100	100	94	91	91
Polychaete larvae	No./m²	140(0.1) NS	71(0.1) NT	227 (0.1)**	2,835 (1.1)*	577 (0.3) NS	1,205 (0.8)
	No./m³	3	1	4	57	12	26
	% frequency	76	81	88	97	85	74
Total copepods	No./m²	49,149(28.3)NS	38,212(78.1) NT	89,074(46.2)*	159,725(60.0) NS	191,772 (84.6)*	96,930(61.8)
	No./m³	1,089	986	1,879	2,260	4,930	2,047
Total chaetognaths	No./m²	1,934(1.1) NS	1,721(3.5) **	797(0.4)**	2,627(1.0) NS	3,502(1.5) NS	2,393(1.5)
	No./m³	34	31	12	53	94	43
Total "others"	No./m²	122,617(70.6)**	8,975(18.4) NT	103,115(53.4) NS	104,226(39.1)**	31,386(13.8) NS	57,401(36.6)
	No./m³	3,441	215	1,582	2,138	733	1,662
Grand total	No./m²	173,697**	49,008 NT	194,238 NS	266,575 NS	226,313 NS	156,472
	No./m³	4,564	1,232	3,473	4,451	5,757	3,752

TABLE 4—Zooplankton taken in onshore (on) (<50 m) and offshore (off) (>50 m) waters of the New York Bight during period 1 (September-November 1974), period 2 (February-May 1975), and period 3 (June-September 1975). Taxa within the major categories (copepods, chaetognaths, others) listed in order of decreasing overall frequency of occurrence. C = common, occurrence in ≥50% of samples; U = unusual, occurrence in ≤50% of samples; R = rare, occurrence in ≤3 samples.

Taxa	Period 1		Period 2		Period 3	
	On	Off	On	Off	On	Off
Copepods:						
Centropages typicus	C	C	C	C	C	C
Pseudocalanus sp.[1]	C	C	C	C	C	C
Calanus finmarchicus	C	C	C	C	C	C
Oithona similis	U	U	C	C	C	C
Paracalanus parvus	C	C	U	C	C	C
O. atlantica	C	C	C	C	U	C
Temora longicornis	C	C	C	U	U	U
Metridia lucens	U	C	C	C	U	C
Clausocalanus pergens	U	C	U	C	U	C
Mecynocera clausi	U	U	U	C	U	C
Candacia armata	C	C	U	U	U	U
Calocalanus tenuis	C	C	—	U	—	C
Oncaea venusta	C	C	R	U	—	U
Pleuromamma borealis	R	U	U	C	—	U
Acartia danae	C	C	—	—	R	U
Nannocalanus minor	C	C	—	—	R	U
A. tonsa	C	U	R	—	U	U
Centropages bradyi	C	C	R	R	—	U
C. hamatus	R	—	U	U	U	U
Rhincalanus nasutus	U	C	R	U	—	R
Eucalanus sewelli	C	C	R	R	—	R
Paracalanus aculeatus	C	C	—	R	—	—
Clausocalanus furcatus	C	C	—	R	R	R
C. jobei	C	C	—	—	—	R
Corycaeus clausi	C	C	—	—	—	—
Scolecithrix danae	C	C	—	R	R	—
A. longiremis	—	—	U	U	U	U
Corycaeus speciosus	C	C	—	—	—	R
T. stylifera	C	C	—	—	—	—
C. danae	—	—	U	U	—	—
Tortanus discaudatus	—	—	U	U	U	—
Calocalanus styliremis	R	—	R	U	—	U
A. hudsonica	R	—	U	R	R	—
Oithona plumifera	C	R	—	—	—	—
R. cornutus	U	U	—	—	—	—
Oncaea mediterranea	U	U	—	—	—	—
E. pileatus	U	U	R	—	—	R
Labidocera aestiva	U	R	—	—	U	R
Aetideus armatus	—	R	—	R	—	U
Paracalanus crassirostris	R	—	—	—	U	U
Corycaeus venustus	R	U	—	R	—	R
Euchaeta marina	U	U	—	R	—	R
Undinula vulgaris	R	U	—	—	R	—
Calocalunus pavo	—	U	—	—	—	—
Ischnocalanus plumulosus	—	U	—	—	—	—
Calanus tenuicornis	R	R	—	R	R	R
O. conifera	R	U	—	—	—	—
Macrosetella gracilis	R	U	—	—	—	—
Clausocalanus parapergens	—	R	—	R	—	R
Sapphirina angusta	R	U	—	—	—	—
C. paululus	—	—	—	R	—	R
Eucalanus subtenuis	R	U	—	—	—	—
Pleuromamma robusta	—	—	—	—	—	R
Faranula gracilis	—	R	—	—	—	—
Calanus helgolandicus	R	—	—	—	R	R
Paracalanus pygmaeus	—	—	—	R	R	R
E. hyalinus	R	U	—	—	—	—
E. crassus	R	R	—	R	—	R
F. carinata	R	—	—	—	—	R
Clausocalanus lividus	—	R	—	R	—	R
Copilia mirabilis	—	R	—	—	—	—
Heterorhabdus norvegicus	—	—	—	—	—	R
H. papilliger	—	R	—	—	—	—
Clausocalanus arcuicornis	—	R	—	—	—	—
L. acutifrons	—	—	—	—	—	R
Corycaeus latus	R	R	—	—	—	—
Anomolocera opalus	—	—	—	—	R	R
Scolecithricella minor	—	—	—	—	—	R
Neocalanus gracilis	—	—	—	—	—	R
O. minuta	—	—	—	R	—	—
Clausocalanus mastigophorus	R	R	—	—	—	—
Corycaeus catus	R	—	—	—	—	—
C. elongatus	R	R	—	—	—	—
Pontella pennata	R	—	—	—	—	—
Sapphirina opaline	—	R	—	—	—	—
Lucicutia flavicornis	—	R	—	—	—	—
Calocalanus pavonius	—	R	—	—	—	—
Scolecithricella vittata	—	R	—	—	—	—
Centropages velificatus	—	—	—	—	—	R
Paracalanus pusillus	—	—	—	—	—	R
Microsetella norvegica	R	—	—	—	—	—
Chiridius obtusifrons	—	—	—	—	—	R
Lubbockia squillimania	—	—	—	—	—	R
S. tenuiserrata	—	—	—	—	—	R
Scottocalanus securifrons	—	—	—	—	—	R
Sapphirina ovatolanceolata	—	—	—	—	—	R
P. quasimodi	—	R	—	—	—	—
Scottocalanus thomasi	—	—	—	—	—	R
Chaetognaths:						
Sagitta elegans	C	C	C	C	C	C
S. serratodentata	C	C	C	C	U	C
S. enflata	C	C	R	U	R	U
Pterosagitta draco	R	U	R	—	—	R
Eukrohnia hamata	—	—	—	R	—	R
S. maxima	—	—	R	R	—	R
S. hexaptera	R	R	—	R	—	R
S. decipiens	—	R	—	—	—	R
S. hispada	—	R	—	—	—	—
E. fowleri	—	R	—	—	—	—
Others:						
Pteropods	C	C	C	C	C	C
Appendicularians	C	C	C	C	C	C
Medusae	C	C	C	C	C	C
Decapod larvae	C	C	U	U	C	C
Polychaete larvae	C	C	C	C	C	C
Bivalve veligers	C	C	C	C	C	C
Euphausiid furcila stages	U	C	C	C	U	C
Gastropod veligers	—	R	C	C	C	C
Ectoproct larvae	C	C	C	C	U	U
Hyperiid amphipods	C	C	U	U	U	C
Copepod nauplii	U	C	C	C	U	U
Evadne spp.	C	U	U	U	C	C
Anthozoan larvae	U	U	U	U	U	C
Euphausiid calyptopsis stages	R	C	U	C	R	C
Doliolids	C	C	—	—	C	C
Plutei	C	U	U	U	U	R
Siphonophores	C	C	R	R	U	U
Penilia avirostris	C	U	—	R	U	U
Conchoecia spp.	U	C	R	U	—	U
Euphausiid nauplii	—	U	R	U	R	U
Barnacle cyprises	—	—	U	U	U	U
Heteropods	U	U	—	—	—	—
Podon spp.	U	—	U	—	R	R
Salps	—	U	—	—	—	U
Barnacle nauplii	—	—	R	U	—	U
Stomatopod larvae	R	—	—	—	R	—

[1]Atlantic representatives of the genus *Pseudocalanus* are not adequately described. They are being studied by B. Frost, Department of Oceanography, University of Washington, Seattle.

warmwater oceanic distributions (Pierce 1953; Grice and Hart 1962; Jefferies 1967; Pennell 1976; Fleminger and Hulsemann 1977).

Mean Abundance, Frequency, Average Rank, and Dominance

We calculated mean abundances for various taxa and found that copepods, on the average, composed 62% of the zooplankton in our samples (Table 2). Pteropods and gastropod veligers together contributed 15% to the total, and cladocerans (*Penilia avirostris* plus *Evadne* spp.) and urochordates (doliolids and appendicularians) yielded another 10 and 6%, respectively. No other group (e.g., echinoderm plutei, medusae, polychaete larvae, chaetognaths), on the average, composed more than about 1% of the zooplankton. At the species level, *Pseudocalanus* sp. and *Centropages typicus* were codominant in 1974-75, their annual mean abundances (number/square meter) each equaling approximatesly 13% of the annual mean for total zooplankton. Pteropods composed another 13% of the zooplankton, and these consisted almost exclusively of one species, *Limacina retroversa* (Wormuth[4]). *Paracalanus parvus, Penilia avirostris, Calanus finmarchicus,* and *Temora longicornis* each composed between 5 and 10% of total zooplankton over the period, and several other taxa had values exceeding 1% (Table 2).

In addition to mean standing stocks and concentrations, we calculated frequency of occurrence, average rank (rank of most abundant taxon in a sample = 1), and an index of dominance (Fager and McGowan 1963) for the 20 taxa having the highest mean abundance in our samples (Table 2). These measures showed similar trends, and, in general, frequency of occurrence and dominance tended to decline and average rank to increase as mean abundance decreased. There were, however, a number of exceptions to this pattern. For instance, the highly seasonal species *P. avirostris* and *T. longicornis* had high mean abundances but disproportionately low frequency and dominance values and high average ranks. Conversely, other taxa, which were seldom abundant, nevertheless occurred frequently (e.g., *S. elegans, O. atlantica,* polychaete larvae, medusae).

[4]J. H. Wormuth, Department of Oceanography, Texas A&M University, College Station, pers. commun. August 1978.

Seasonality in Abundance

Total zooplankton in the New York Bight declined nearly fourfold in mean abundance between late summer (September) and autumn (October-November) 1974 (Table 3), primarily because of a drastic decline in the abundance of *P. avirostris* after September. In 1975, numbers of total zooplankton did not vary as greatly between seasons, and the highest mean value (April-May) differed from the lowest (August-September) by less than a factor of two. Copepods were least numerous in winter (February-March), but increased through spring (April-May) to an early summer (June-July) peak before declining in late summer (August-September). Other zooplankton combined exceeded copepods in mean abundance only during winter, and this primarily was due to the large standing stocks of the pteropod *L. retroversa* present in the Bight during that period.

We calculated mean abundances by season for the 20 taxa having the highest overall mean values in our samples (Table 2) and found that most of these taxa underwent marked and often statistically significant ($P<0.05$) seasonal fluctuations in standing stock (Table 3). *Penilia avirostris,* doliolids, echinoderm plutei, and *Acartia tonsa* reached maximum or near maximum levels of abundance in late summer 1974 and again in late summer 1975. With the exception of echinoderm plutei, these taxa were virtually absent from our samples during the intervening winter and spring. The relatively low numbers of small copepods in 1974 may have been due to escapement through the coarse mesh (333 μm) nets used then. We found that *Paracalanus parvus, Pseudocalanus* sp., *O. similis,* and *Clausocalanus pergens* were significantly less abundant (paired sample t-test, $P<0.05$) in collections from 60 cm diameter 333 μm mesh nets than in simultaneous samples from 20 cm diameter 253 and 223 μm mesh nets.

Only 1 taxa (*L. retroversa*) peaked in winter 1975, but 10 taxa (*Pseudocalanus* sp., *Calanus finmarchicus, O. similis, Metridia lucens, Clausocalanus pergens, Evadne* spp., appendicularians, gastropod veligers, medusae, and polychaete larvae) reached their highest levels of abundance during spring 1975. *Centropages typicus, T. longicornis,* and *S. elegans* attained maximum levels of abundance in early summer, and *Paracalanus parvus* peaked in late summer 1975. Among the 20 taxa listed in Table 3, *O. at-*

lantica varied the least in mean abundance during the study, showing only slight increases during spring and late summer 1975.

Onshore-Offshore Distribution

Several of the more abundant zooplankton taxa in the New York Bight showed statistically significant ($P<0.05$) differences in mean standing stocks between the onshore (<50 m) and offshore (>50 m) sectors of the region (Table 5). Taxa which on the average were significantly more abundant onshore during 1974-75 were *C. typicus, Penilia avirostris, T. longicornis, Evadne* spp., *A. tonsa,* and doliolids. Those which were significantly more abundant offshore were *Calanus finmarchicus, O. similis, O. atlantica, M. lucens,* and *Clausocalanus pergens.* Significant onshore-offshore differences on an annual basis were not observed for *Pseudocalanus* sp., pteropods, *Paracalanus parvus,* appendicularians, gastropod veligers, echinoderm plutei, medusae, and *S. elegans.* Neither total copepods nor total chaetognaths differed significantly between the two regions, but other zooplankton combined were significantly more abundant offshore (Table 5).

Substantial seasonal changes occurred in the onshore-offshore distribution of many of the aforementioned taxa (Figure 2). Certain copepod species which peaked or were otherwise very abundant in the offshore region during winter and spring were much less abundant onshore at those times. However, during the summer, onshore stocks of these species increased to levels approaching those in offshore waters. Species exhibiting this pattern were *M. lucens, C. pergens, O. atlantica, Calanus finmarchicus,* and *P. parvus* (Figure 2). Several other taxa which reached maximum levels of abundance during the spring tended to be equally abundant onshore and offshore during most times of the year. This group of ubiquitously abundant taxa included *Pseudocalanus* sp., *O. similis, S. elegans,* medusae, appendicularians, pteropods, gastropod veligers, and polychaete larvae (Figure 2). Doliolids and the coastal-estuarine species *Penilia avirostris, T. longicornis,* and *A. tonsa* all peaked in the onshore environment during summer or autumn and were seldom, if ever, abundant offshore (Figure 2). Although *Centropages typicus* also reached its highest levels of abundance onshore during the summer, it was usually abundant offshore as well, especially during March and April (Figure 2). Echinoderm plutei peaked in onshore waters during autumn 1974 but also exhibited a secondary offshore peak during spring 1975 (Figure 2). *Evadne* spp. exhibited maxima in both the onshore and offshore environments during spring and summer 1975 but were abundant only onshore during autumn 1975 (Figure 2).

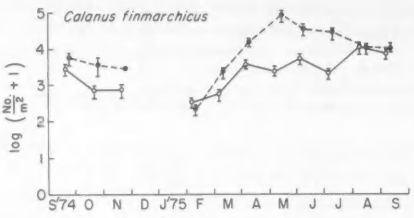
Zooplankton Maxima, Phytoplankton Blooms, and Temperature

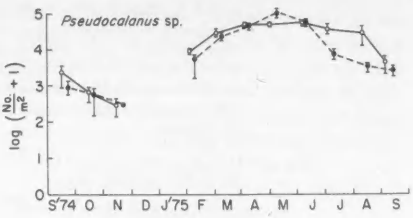
We observed distinct peaks in zooplankton abundance in both onshore and offshore environments in 1975 (Figure 3). In the offshore region, there were two maxima, in March and May. The March peak was dominated by *L. retroversa* which composed nearly 60% of all offshore zooplankton during that month. The remaining 40% of offshore zooplankton in March was composed primarily of the copepods *Pseudocalanus* sp., *O. similis, Paracalanus parvus,* and *M. lucens.* The May maximum was dominated by *Pseudocalanus* sp., *Calanus finmarchicus,* and *O. similis,* and these species tended to be most abundant over the outer shelf at the eastern end of the study area (e.g., stations F3, F5, G2, G4). The March pteropod-dominated maximum occurred similtaneously with the beginning of the spring phytoplankton bloom when chlorophyll *a* standing stock biomass (milligrams/square meters) was high (Figure 3) and discrete depth chlorophyll *a* concentrations exceeded 4 μg/l throughout the water column at virtually all stations. However, during May when copepods peaked in abundance offshore, the phytoplankton bloom was in decline (Figure 3). In the offshore region, water temperatures in the upper 20 m remained low ($\leq$10° C) through May.

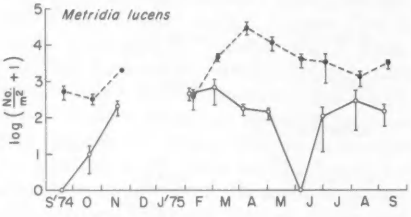
We observed a single peak in zooplankton abundance in the onshore environment during 1975 (Figure 3). This peak occurred in July and was the result of marked increases in the abundance of *Centropages typicus* and *T. longicornis.* In July, these two species constituted about 67% of all onshore zooplankton and were especially abundant at stations near the apex of the Bight and off the New Jersey coast (e.g., A2, A4, B3, B5). The early summer rise in *C. typicus* and *T. longicornis* stocks occurred during a period when surface water temperatures rose from about 10° to 20° C but when onshore chlorophyll *a* biomass was low (Figure 3). At other times during this study various other taxa were dominant onshore, e.g., *Penilia*

TABLE 5.—Onshore-offshore variations in mean abundance (no./m² and no./m³) and frequency of occurrence (% of samples) of the 20 most abundant zooplankton taxa in the New York Bight, 1975, listed in order of overall mean abundance. Onshore: depth <50 m, offshore: depth >50 m. Values in parenthesis after no./m² values are percents of total zooplankton. Asterisks indicate significant differences (Fisher-Behrens test, Campbell 1967) in mean no./m² between onshore and offshore (* = $P<0.05$, ** = $P<0.01$, NS = not significant).

No. samples (chaetognaths)		Onshore 100	Offshore 78
No. samples (copepods, others)		99	84
Taxa	Item		
Pseudocalanus sp.	No./m²	26,308(13.1) NS	24,691(14.9)
	No./m³	713	295
	% frequency	91	92
Pteropods	No./m²	21,487(10.7) NS	30,298(18.2)
	No./m³	564	379
	% frequency	99	98
Centropages typicus	No./m²	35,637(17.8)**	12,759(7.7)
	No./m³	1,071	165
	% frequency	98	96
Paracalanus parvus	No./m²	14,668(7.3) NS	16,136(9.7)
	No./m³	400	208
	% frequency	67	89
Penilia avirostris	No./m²	26,829(13.4)**	217(0.1)
	No./m³	836	4
	% frequency	31	24
Temora longicornis	No./m²	20,455(10.2)**	651(0.4)
	No./m³	681	9
	% frequency	76	43
Calanus finmarchicus	No./m²	3,604(1.8)**	20,251(12.2)
	No./m³	82	220
	% frequency	85	98
Oithona similis	No./m²	5,415(2.7)**	11,686(7.0)
	No./m³	151	140
	% frequency	85	77
Appendicularians	No./m²	6,576(3.2) NS	7,666(4.6)
	No./m³	157	89
	% frequency	80	88
Gastropod veligers	No./m²	6,556(3.2) NS	2,804(1.7)
	No./m³	173	41
	% frequency	58	65
Evadne spp.	No./m²	5,891(2.9)**	1,557(0.9)
	No./m³	149	22
	% frequency	49	41
Doliolids	No./m²	6,497(3.2)*	185(0.1)
	No./m³	165	2
	% frequency	29	34
Metridia lucens	No./m²	178(0.1)**	5,232(0.3
	No./m³	4	41
	% frequency	37	83
Plutei	No./m²	3,591(1.7) NS	680(0.4)
	No./m³	86	9
	% frequency	35	25
O. atlantica	No./m²	564(0.3)**	3,646(2.2)
	No./m³	13	31
	% frequency	57	90
Clausocalanus pergens	No./m²	161(0.1)**	3,777(2.3)
	No./m³	4	31
	% frequency	28	78
Medusae	No./m²	1,454(0.7) NS	1,378(0.8)
	No./m³	35	19
	% frequency	76	73
Acartia tonsa	No./m²	2,432(1.2)*	63(<0.1)
	No./m³	78	1
	% frequency	35	11
Sagitta elegans	No./m²	1,407(0.7) NS	1,187(0.7)
	No./m³	34	17
	% frequency	95	96
Polychaete larvae	No./m²	989(0.5) NS	946(0.3)
	No./m³	26	13
	% frequency	65	68
Total copepods	No./m²	115,284(57.7) NS	113,104(68.2)
	No./m³	3,358	1,284
Total chaetognaths	No./m²	2,175(1.1) NS	2,282(1.4)
	No./m³	52	32
Total "others"	No./m²	82,510(41.3)*	50,396(30.4)
	No./m³	2,663	626
Grand total	No./m²	119,943 NS	165,590
	No./m³	6,073	1,942


Calanus finmarchicus
log (No./m² + 1)
0 1 2 3 4 5
S'74 O N D J'75 F M A M J J A S


Pseudocalanus sp.
log (No./m² + 1)
0 1 2 3 4 5
S'74 O N D J'75 F M A M J J A S


Metridia lucens
log (No./m² + 1)
0 1 2 3 4 5
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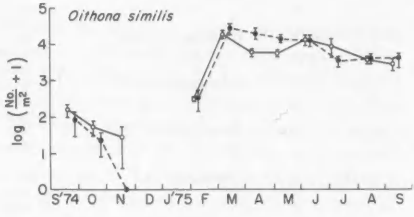
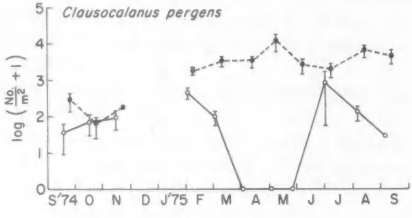

Oithona similis
log (No./m² + 1)
0 1 2 3 4 5
S'74 O N D J'75 F M A M J J A S


Clausocalanus pergens
log (No./m² + 1)
0 1 2 3 4 5
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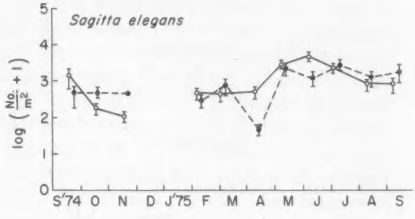
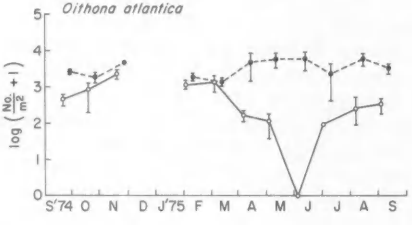

Sagitta elegans
log (No./m² + 1)
0 1 2 3 4 5
S'74 O N D J'75 F M A M J J A S


Oithona atlantica
log (No./m² + 1)
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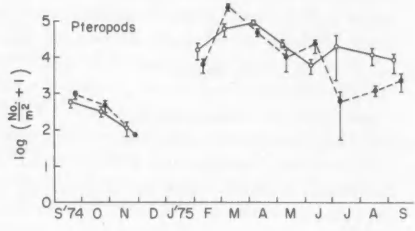
Pteropods
log (No./m² + 1)
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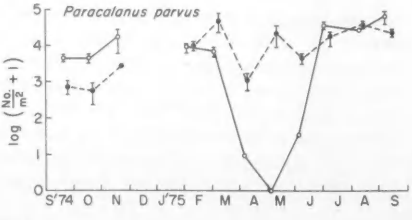
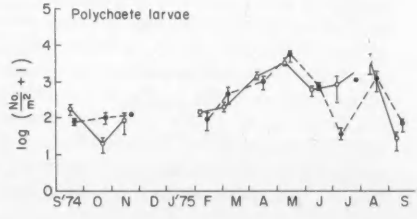

Paracalanus parvus
log (No./m² + 1)
0 1 2 3 4 5
S'74 O N D J'75 F M A M J J A S


Polychaete larvae
log (No./m² + 1)
0 1 2 3 4 5
S'74 O N D J'75 F M A M J J A S

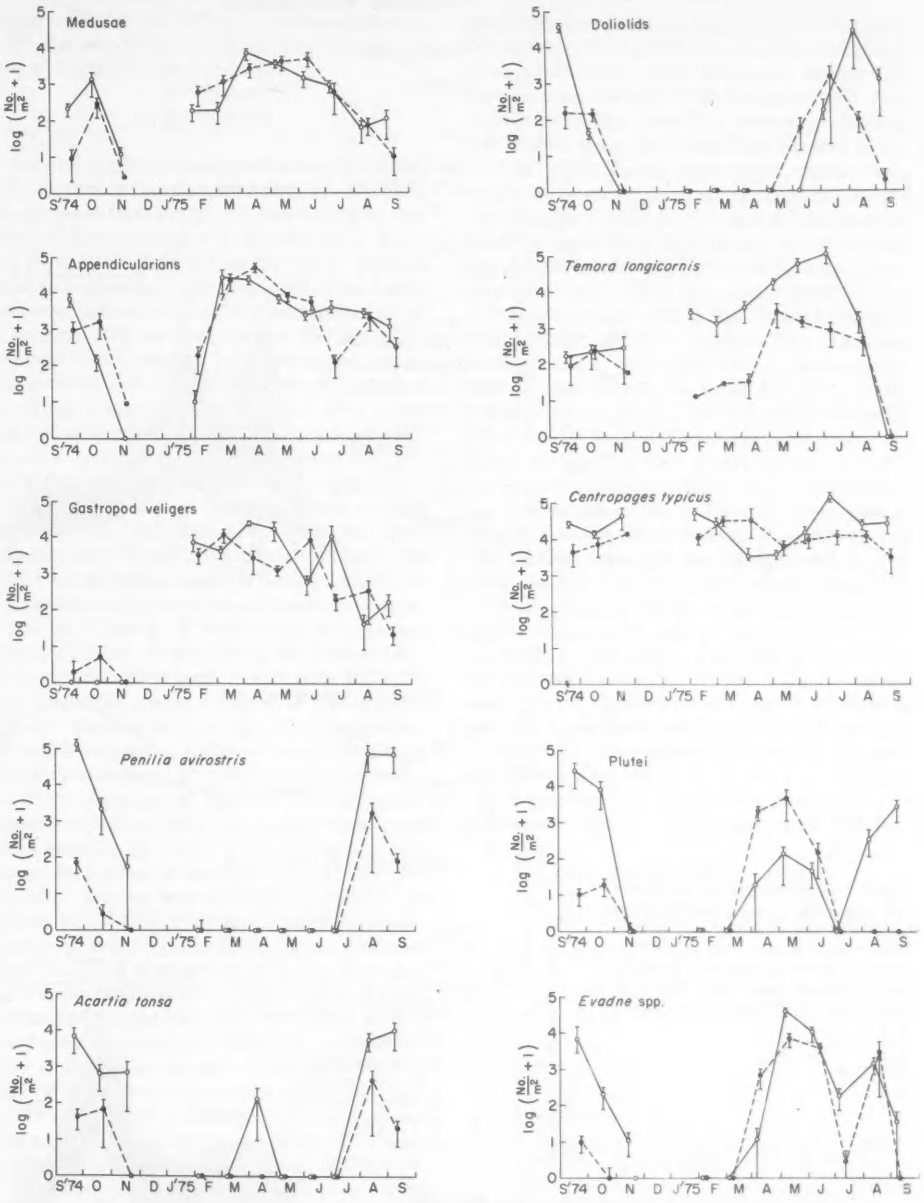


FIGURE 2.—Onshore (<50 m) and offshore (>50 m) monthly mean abundances of 20 most abundant zooplankton taxa in the New York Bight, September 1974-September 1975. Circles = onshore means; dots = offshore means; vertical bars = 1 SE above and below mean.

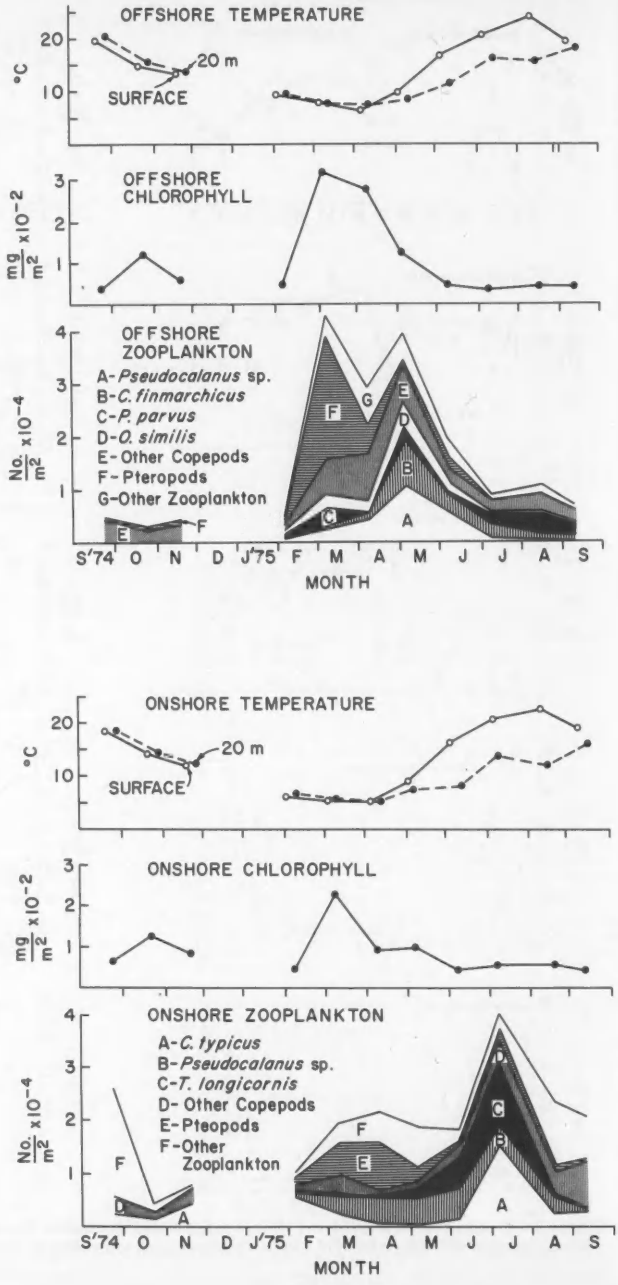


FIGURE 3.—Onshore (<50 m) and offshore (>50 m) monthly means for temperature at surface and 20 m, chlorophyll *a* integrated water column biomass, and zooplankton abundance (showing cumulative contribution of dominant taxa) in the New York Bight, September 1974-September 1975.

avirostris (September 1974), *L. retroversa* (March, April), *Pseudocalanus* sp. (May), and *Paracalanus parvus* (August, September 1975).

DISCUSSION

Previous zooplankton studies in the New York Bight have been based on relatively few samples, usually taken from a restricted area over a limited period of time (cf. review in Malone 1977). Grice and Hart's (1962) study is closest to ours in taxonomic coverage, net mesh size, geography, and quantitative analysis. They collected a total of 14 samples with vertically hauled 230 μm mesh nets from New York Bight shelf waters on cruises in September and December 1959 and March and July 1960. These samples were part of a larger study of zooplankton along a transect between Montauk, N.Y., on eastern Long Island and Bermuda. Comparison of mean concentrations of several abundant species of copepods in their samples (table 4, Grice and Hart 1962) with our mean concentration values (Table 2) is informative. The eight most abundant copepods during 1959-60 (in order of decreasing abundance: *Pseudocalanus* sp., *C. typicus, O. similis, T. longicornis, Paracalanus parvus, Calanus finmarchicus, M. lucens, Candacia armata)* correspond closely with the eight most abundant species in 1974-75 (*Centropages typicus, Pseudocalanus* sp., *T. longicornis, Paracalanus parvus, Calanus finmarchicus, O. similis, Acartia tonsa, O. atlantica)*. Furthermore, the mean densities of the two most abundant copepods in both studies, *Centropages typicus* and *Pseudocalanus* sp., were very similar for both species during the two periods (i.e., the mean density of *C. typicus* was 450/m³ in 1959-60 and 650/m³ in 1974-75; the mean density of *Pseudocalanus* sp. was 560/m³ in 1959-60 and 520/m³ in 1974-75). This comparison suggests that zooplankton in the New York Bight had not changed substantially in the 15 yr between the two studies. The degree of similarity is somewhat surprising in view of the evidence that considerable year-to-year variations may occur in the timing, duration, and amplitude of abundance maxima in important zooplankton taxa (Bigelow and Sears 1939; Sears and Clarke 1940).

Grice and Hart (1962) observed an influx of warmwater oceanic species into the New York Bight in September 1959, and this is similar to the high incidence of subtropical-tropical species in autumn 1974 and summer 1975. This apparently annual phenomenon is probably associated with intrusions of the Gulf Stream over the continental slope which occur most frequently during the warm seasons (Wright 1976; Bowman 1977). Our hydrographic data reveal the occurrence of salinities (≥36%) characteristic of Gulf Stream water (Wright 1976) in the slope region during September 1974, and in June, August, and September 1975 (Figure 4), and the National Environmental Satellite photos show Gulf Stream water impinging along the outer edge of the study area in August 1974 and in May, July, and August 1975.

A shoreward increase in the abundance of several common offshore copepods (e.g., *Calanus finmarchicus, O. atlantica, Clausocalanus pergens, M. lucens*) also occurred during warm portions of the year. This onshore increase in abundance of common forms and the frequent occurrence over the shelf of less common oceanic species are probably the result of shoreward mixing of slope water with shelf water. Slope water is thought to move onshore along isopycnals during late summer and autumn (Wright and Parker 1976; Gordon et al. 1977), and during September 1974 we observed slope water (35‰ ≤salinity <36‰, Wright 1976) on the shelf (Figure 4).

Limacina retroversa, Pseudocalanus sp., *O. similis,* and *Calanus finmarchicus,* the species responsible for zooplankton abundance maxima in the New York Bight during spring 1975, are low-temperature forms whose distributions are centered north of the region (Fish 1936a, b, c; Redfield 1939; Bigelow and Sears 1939; Fleminger and Hulsemann 1977). Their geographical distribu-

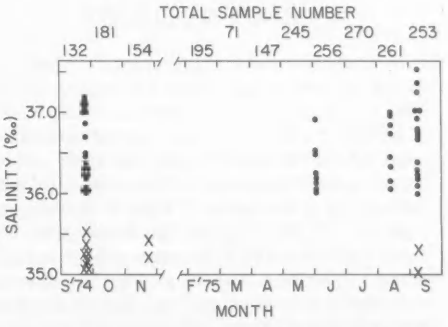


FIGURE 4.—Occurrences of Gulf Stream water (salinity ≥36‰) over slope (≥100 m), and of slope water (35‰<salinity<36‰) over the shelf in the New York Bight, September 1974-September 1975. Dots = Gulf Stream salinities over slope; × = slope salinities over shelf.

tions and the generally southward flow along this sector of the shelf (Bumpus 1973) suggest that a high proportion of individuals occurring in the Bight are advected into the region from the northeast. Irrespective of the origin of these populations, it can be assumed that they were major consumers of the spring phytoplankton bloom in 1975.

Centropages typicus and *Temora longicornis* are warm temperate species (Fleminger 1975), and their abundance in the New York Bight appears to be strongly influenced by temperature. Lawson (1969) found that *C. typicus* eggs failed to hatch when maintained at 5°-6° C, the prevailing water temperature in February through May (Figure 3), and Bigelow and Sears (1939) reported a northward seasonal shift in abundance of *C. typicus* beginning in the Chesapeake Bay-Delaware Bay region in the spring, progressing to the New York area in July, and finally reaching coastal waters off New England in autumn. The geographical distribution of *T. longicornis* corresponds closely to that of *C. typicus* (Fleminger 1975), and it is likely that it exhibits similar seasonal trends in abundance. In the New York Bight in 1975, *C. typicus* and *T. longicornis* increased in abundance from April to July as water temperature rose from about 5° to 20° C (Figure 3). These species appear to be especially well adapted for exploitation of coastal environments where high food levels persist into the warm season. Their peak abundances in 1975 occurred in or near the apex of the Bight where primary production in July can exceed 1-3 g C/m^2 per day (Malone 1976).

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DISTRIBUTION AND CATCH COMPOSITION OF JONAH CRAB, *CANCER BOREALIS*, AND ROCK CRAB, *CANCER IRRORATUS*, NEAR BOOTHBAY HARBOR, MAINE[1]

JAY S. KROUSE[2]

ABSTRACT

An analysis of research and commercial catch data of Jonah crab, *Cancer borealis*, and rock crab, *C. irroratus*, collected near Boothbay Harbor, Maine, revealed dissimilarities in the distribution of the two species. Jonah crabs were more numerous at the deeper, seaward sampling sites with rocky substrates, while rock crabs were more abundant on soft mud bottoms of the shallower estuarine stations. Distribution of both species is dependent upon the environmental factors of temperature, depth, and substrate type. Absence of Jonah crabs <67 mm carapace width in all collections, indicates that, unlike the rock crab, the nursery areas of the Jonah crab are not in nearshore waters. Sex ratios varied seasonally and spatially for rock crabs and seasonally for Jonah crabs. These variations seem to be related to changes in local abundance as the result of movement in association with the reproductive and molting cycles.

Jonah crab, *Cancer borealis*, and rock crab, *C. irroratus*, make up a small but increasingly important commercial fishery along the Maine coast. Since 1966, the price per pound of crabs paid to the fisherman has increased from 4¢ to 12¢ (Figure 1). As a result the Maine lobstermen have been selling their incidental catches of crabs to offset increasing operational costs (bait, fuel, etc.). In view of the current retail price of American lobster, *Homarus americanus*, which often exceeds $3.00/lb, the value of the very palatable crab may be expected to continue to increase. In fact, some dealers are now paying 20¢ to 25¢/lb for crab.

Despite the present economic value (reported 1977 landed value was $142,106) of Maine's crab fishery and its potential for future growth, there is little information on the biology of either of the cancrid crabs. While several investigators have studied various aspects of the life history of *C. irroratus*, very little work has been done on *C. borealis* other than by Haefner (1977) and Carpenter (1978) on the distribution and biology of *C. borealis* on the continental shelf of the Mid-Atlantic Bight and by Sastry (1977) on the larval development of *C. borealis*.

To supplement these studies, I have: 1) examined the size and sex composition and distribution of Jonah crabs in commercial and research catches in Maine waters; 2) described the width-weight relationship of the Jonah crab; and 3) compared the distribution, size, and sex composition of Jonah and rock crabs from commercial and research catches.

METHODS

Jonah crabs were caught incidental to the lobster sampling program of the Maine Department of Marine Resources during which vinyl-coated wire (2.54 × 2.54 cm mesh) and conventional wooden lobster traps were fished at nine locations (Figure 2) near Boothbay Harbor, Maine, from July 1968 to December 1974.

At the time of capture, each crab was sexed and measured. Carapace width (CW), distance between the two outermost notches on the anterolateral border of the carapace, was recorded to the nearest millimeter.

Width-weight relations were calculated for 110 male (89-160 mm CW) and 90 female (96-131 mm) Jonah crabs caught by commercial fishermen near Boothbay Harbor, 1973 through 1976. Wet weights were recorded to the nearest 10 g. Linear regression of weight on carapace width was fitted by the method of least squares to logarithmically (base 10) transformed data, and analysis of covariance was used to evaluate the regression coefficients of males and females for differences.

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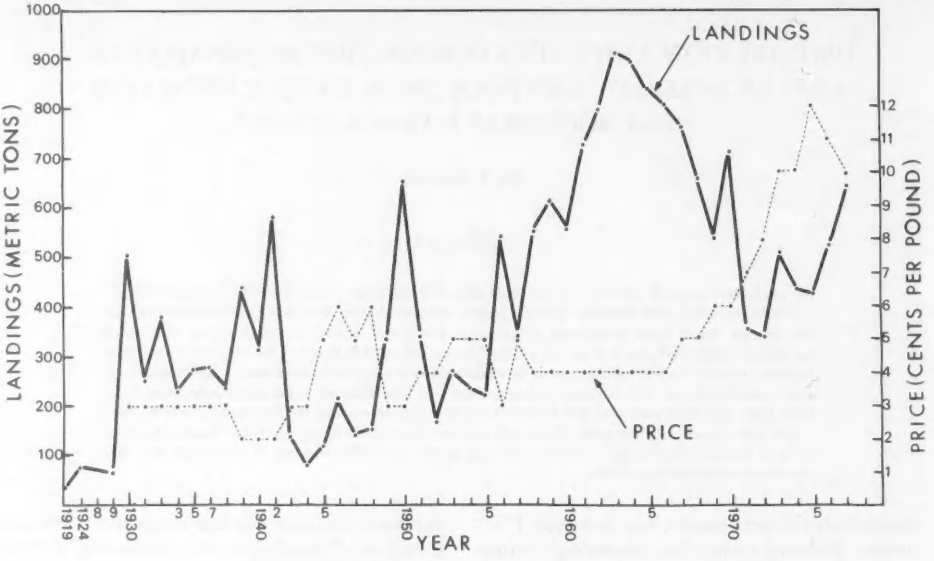


FIGURE 1.—Catch and ex-vessel price of Jonah and rock crabs (species combined) landed in Maine, 1919-77.

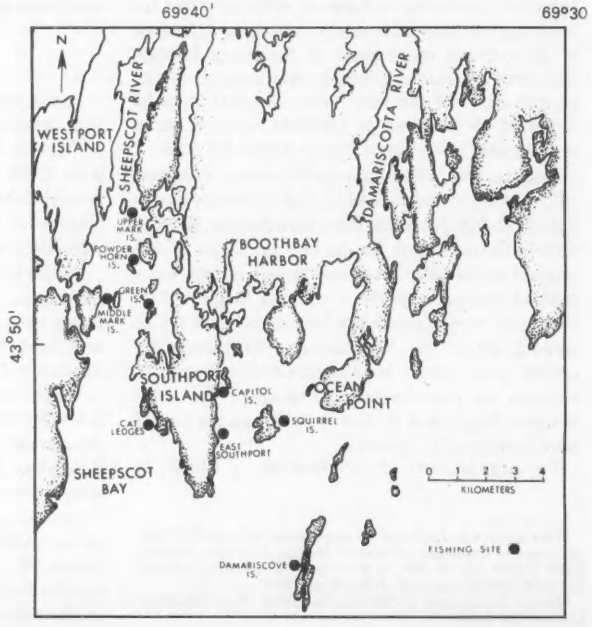


FIGURE 2.—Boothbay Harbor region and location of sampling sites.

Additional commercial catch data were provided by Joel Cowger, Maine Department of Marine Resources, West Boothbay Harbor, Maine, who obtained measurements of 299 commercially caught Jonah crabs from the Maine coast (September 1977-March 1978). Carapace widths were measured between the tips of the outermost anterolateral spines. These long carapace width measurements can be converted to short carapace width (distance between notches) by the linear regression $Y = -1.669 + 0.973X$ where Y = short CW and X = long CW (Carpenter 1978).

RESULTS AND DISCUSSION

Size Composition

Jonah crabs captured with research traps (mean 104.8 mm CW for females and 113.7 mm for males) were significantly smaller (t-test, $P<0.01$) than those crabs commercially landed at either Boothbay Harbor (mean 114.0 mm CW for females and 128.6 mm for males) or at other Maine ports (mean 114.0 mm CW for females and 141.1 mm for males) (Figures 3-5). At first it was thought that disparities in size composition might be associated to variations in selectivity of the research and commercial gear for crabs <95 mm CW; however, since similar proportions of small crabs appeared in both the research and commercial catches (Figures 3-5), the effects of gear selectivity must be minimal. The near total absence of crabs <95 mm CW in the commercial catch from Boothbay Harbor (Figure 4) was the result of fishermen discarding the smaller crabs before their landed catches were measured; whereas, the catches shown in Figures 3 and 5, which were measured at sea, included all crabs caught. Thus, I attribute these size disparities to spatial variations in the distribution of different size crabs. For instance, research traps were fished at depths of 3-20 m, whereas, most commercial traps were fished at depths of 12-91 m. In support of this contention, different size groups of Jonah crabs have been observed to be distributed within the Mid-Atlantic Bight according to depth (Haefner 1977; Carpenter 1978).

Male Jonah crabs averaged larger than females in all catches (Figures 3-5); similarly, male rock crabs generally averaged larger than females (Krouse 1972). Unlike female rock crabs, which have no commercial value because of their small size (rarely >100 mm CW, Krouse 1972), female Jonah crabs, which approximate the size of male rock crabs, are commercially harvested along with male Jonah crabs.

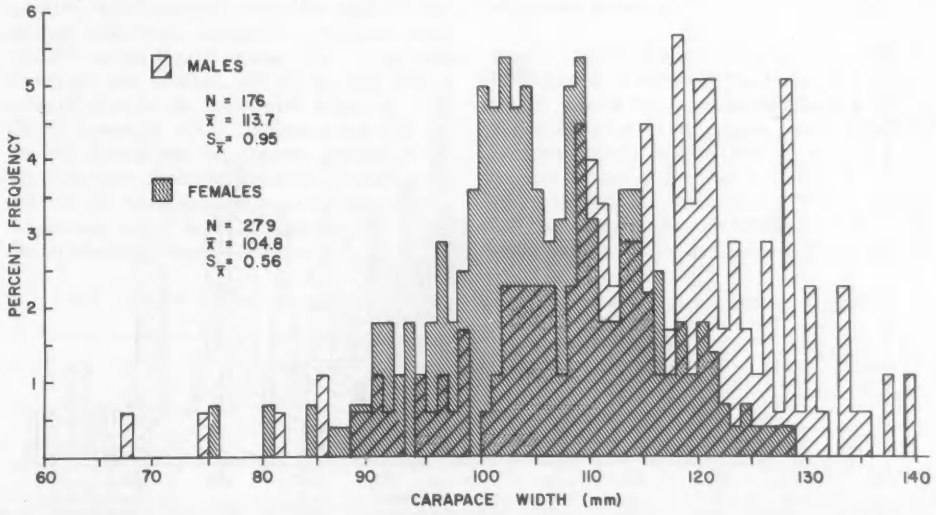


FIGURE 3.—Width-frequency distributions of male and female Jonah crabs caught with research traps in the Boothbay Harbor region, 1968-74.

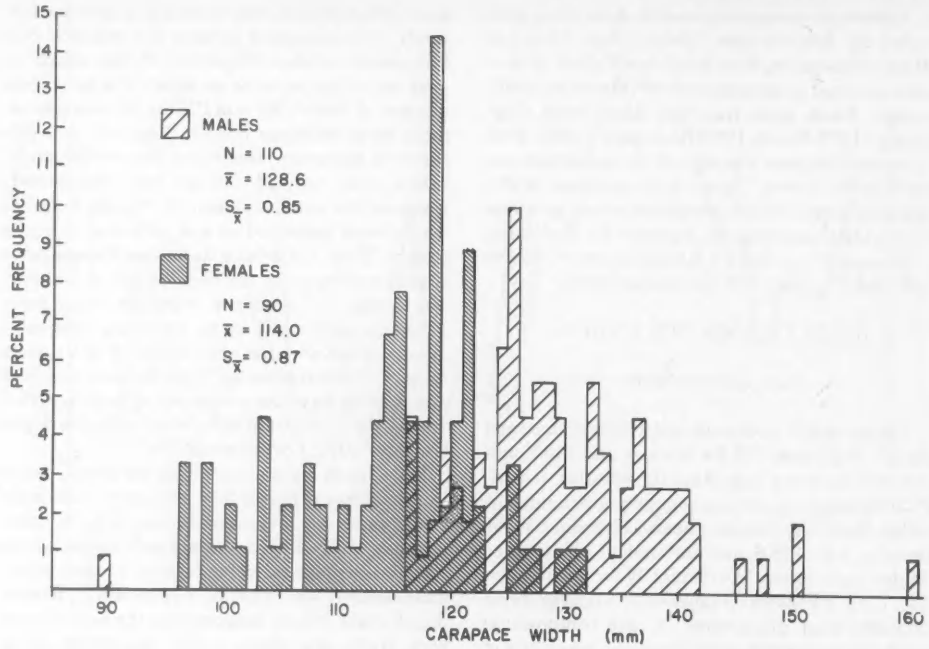


FIGURE 4.—Width-frequency distributions of male and female Jonah crabs caught by commercial fishermen in the Boothbay Harbor region, 1973-76.

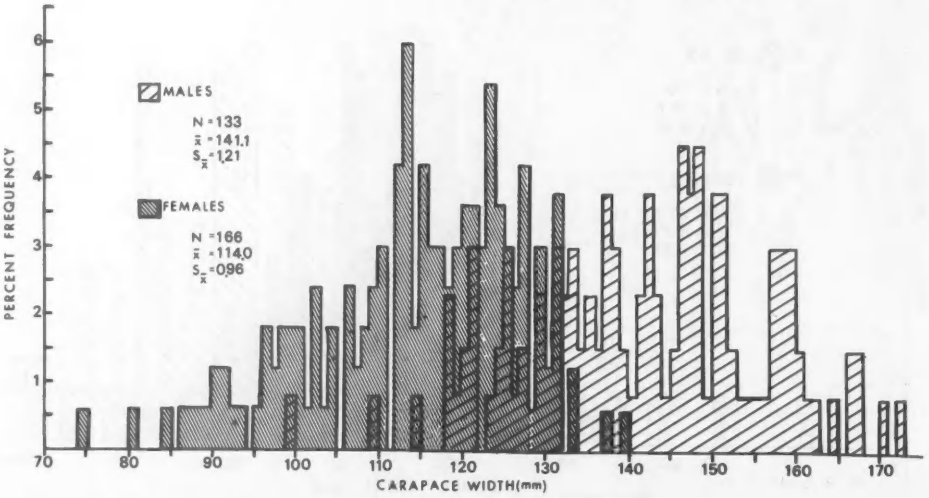


FIGURE 5.—Width-frequency distributions of male and female Jonah crabs caught by commercial fishermen at various locations along the Maine coast, 1977-78.

The total commercial and research catch of 954 Jonah crabs included only 27 (2.8%) individuals <90 mm. This might be related to gear selectivity, but this explanation loses credibility given that numerous rock crabs (equivalent catchability to Jonah crab) from 40 to 60 mm CW have been sampled previously with conventional and modified lobster traps (Krouse 1976). Moreover, the fact that no Jonah crabs <67 mm CW were observed while hand-collecting 2,426 rock crabs (mean 23.9 mm CW) during a 3-yr intertidal study (Krouse 1976) or hauling research gear over a 9-yr period (juvenile rock crabs were frequently seen in traps) is evidence that small Jonah crabs in Maine waters, unlike juvenile rock crabs, inhabit deeper water exclusively. In the Mid-Atlantic Bight, Carpenter (1978) reported that Jonah crabs <30 mm CW were most abundant in depths <150 m, while Haefner (1976) found crabs ≤40 mm CW to be most numerous between 75 and 150 m. Both investigators noted that the maximum abundance of the larger crabs (>40 mm) occured in the 150-400 m strata.

Distribution

From July 1968 through 1974, 459 Jonah crabs were captured in 7,055 trap hauls (0.07 crab/trap haul) with research gear fished near Boothbay Harbor (Table 1). Fluctuations in the catch in association with temporal and spatial variations in fishing effort were assessed by plotting mean monthly values of catch in numbers per trap haul (catch per unit of effort, CPUE) for each fishing area (Figure 6). In areas with relatively high CPUE (average >0.1), catches gradually increased throughout the summer, peaked in the fall, and then diminished rapidly. Because most crabs in the research catch were at least two molt increments larger than the lower size limit of the gear's selectivity range, the seasonal rise in CPUE

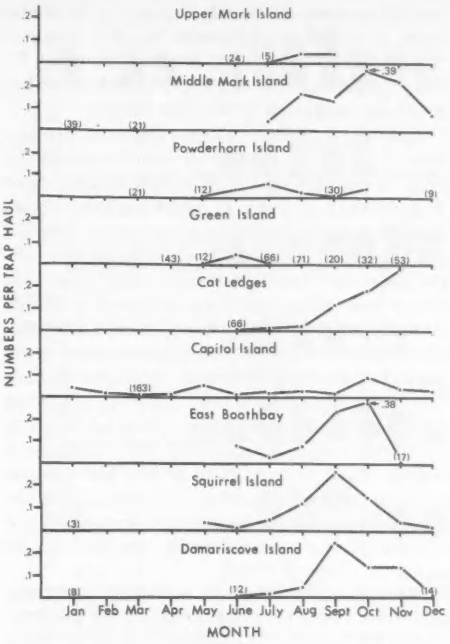


FIGURE 6.—Monthly catch per unit of effort values for Jonah crabs collected at various stations in the Boothbay Harbor region, 1968-74. Number of trap hauls are in parentheses. Catch per unit of effort outliers are marked by arrows.

may be explained by recruits migrating into the fishing areas. Conversely, the decline in CPUE in winter may be attributed to the effects of fishing mortality as well as emigration. Jonah crabs have been reported by Jeffries (1966) to move into the warmer waters of Narragansett Bay, R.I., from spring through fall, followed in winter by a movement to deeper, relatively warmer waters as inshore water temperature declined. The closely re-

TABLE 1.—Trap catch-effort values of Jonah and rock crabs caught in research traps at various stations near Boothbay Harbor, Maine, 1968-74.

Area	Depth range (m)	Substrate	Hauls	Jonah crab		Rock crab	
				Total no. caught	No. per haul	Total no. caught	No. per haul
Upper Mark Island	5-15	Mud	157	5	0.03	645	4.11
Powderhorn Island	3-10	Mud	271	8	0.03	2,062	7.61
Green Island	3-10	Mud	396	4	0.01	1,025	2.59
Middle Mark Island	10-20	Mud-rock outcroppings	522	65	0.12	671	1.29
Cat Ledges	5-15	Sand-bedrock	656	41	0.06	660	1.01
Capitol Island	5-15	Mud	2,794	75	0.03	4,869	1.74
East Southport	5-15	Mud-rock outcroppings	253	30	0.12	318	1.25
Squirrel Island	5-20	Mud-rock outcroppings	1,267	149	0.12	2,674	2.11
Damariscove Island	5-20	Sand-bedrock	739	82	0.11	535	0.72
Total	3-20		7,055	459	0.07	13,459	1.91

lated European edible crab, *C. pagurus*, have also been observed to undertake similar seasonal movements off the coast of England (Brown[3]). Limited population movements of Jonah crabs has also been suggested by Haefner (1977).

Although Jonah crabs were caught at each station, their relative abundance varied markedly by area as reflected by CPUE values which ranged from 0.01 to 0.12 (Table 1). Jonah crabs were more numerous at the generally deeper, more seaward stations (East Southport, Squirrel Island, and Damariscove Island) characterized by rocky substrates and within the Sheepscot River at Middle Mark Island where the fishing area borders relatively deep water (45 m) and the bottom is hard-packed mud interspersed with rock outcroppings. Conversely, Jonah crabs were sparsely distributed at the other stations in the Sheepscot estuary (Upper Mark Island, Green Island, and Powderhorn Island) which in contrast to Middle Mark Island are quite shallow with soft mud bottoms. Thus, the data indicate that the distribution and abundance of Jonah crabs reflects bottom type as well as depth.

Comparisons of CPUE for rock crabs with those for Jonah crabs at different sampling sites revealed an inverse relationship (Table 1). Rock crabs were very abundant at those stations within the Sheepscot River (CPUE: 2.6-7.6) where Jonah crabs were scarce; whereas, at other areas where Jonah crabs were more plentiful rock crabs were less common (CPUE: 0.7-2.1). Based on these observations, rock crabs seem to prefer inshore areas with mud bottoms while Jonah crabs favor seaward locations with rocky substrates. This agrees with Jeffries (1966) findings that the same two cancrid crabs are separated spatially in Narragansett Bay according to bottom type: rock and Jonah crabs inhabit sand and rock substrates, respectively. Interestingly, in the more northern latitudes, juvenile rock crabs, unlike the adults, show preference for coarse, rocky bottoms (Scarratt and Lowe 1972; Krouse 1972; Reilly and Saila 1978), where protection from predators would be optimum.

Distribution of both cancrid crabs is not only related to substrate type and depth, but is also dependent upon water temperature. For example, in the mid-Atlantic region, Carpenter (1978) found Jonah crabs at temperatures from 5° to 15° C with maximum abundance between 6° and 12° C. Similarly, Haefner (1977) reported Jonah crabs to be most numerous in the temperature range of 8°-14° C. The more eurythermal rock crabs have been observed to be widely distributed over the continental shelf of the Mid-Atlantic Bight and most abundant inshore particularly during winter when temperatures are lowest (as low as 2° C) (Musick and McEachran 1972; Haefner 1976). In Chesapeake Bay rock crab abundance increases markedly in winter (2°-8° C) and declines in spring as temperatures warm (Shotton 1973; Terretta 1973). In view of these data, the distribution of the two cancrid crabs along the Maine coast may be further examined in relation to temperature. Rock crabs have been found to be most abundant in shallow nearshore waters where temperatures may vary from near 0° C in winter to 18° C in summer (Welch[4]); whereas, Jonah crabs are more numerous at greater depths where temperatures are more stable. Likewise, in the Gulf of St. Lawrence where the temperature regime is great (−2° to 20° C [Lauzier and Hull[5]]), rock crabs are common and Jonah crabs are nonexistent (Squires 1966; Scarratt and Lowe 1972).

Thus, it appears that the distribution of these congeneric species in the northern part of their range is dependent upon substrate, depth, and temperature.

Sex Ratios

Initially, I examined ratios of male to female Jonah crabs in monthly catches at each fishing site; however, due to the small sample sizes for several of the groups, area catches were combined by month (Table 2). The chi-square test, which was used only when the monthly N was ≥ 10, indicated that July through September ratios deviated significantly ($P = 0.05$) from 1:1. Males dominated in July while during August and September there was a preponderance of females. This shift in sex ratios may be attributed to an apparent movement of female crabs into warmer shoal water during summer and early fall as the result of behavior associated with molting and copulating. The closely related Dungeness crab, *C. magister*, and

[3]Brown, G. G. 1975. Norfolk crab investigations 1969-73. Lab. Leafl. 30, 12 p. Fish. Lab., Lowestoft, Suffolk, England.

[4]W. R. Welch, Marine Resources Scientist, Maine Department of Marine Resources, West Boothbay Harbor, ME 04575, pers. commun. February 1979.

[5]Lauzier, L. M., and J. H. Hull 1969. Coastal station data temperatures along the Canadian Atlantic coast 1921-1969. Fish. Res. Board Can. Tech. Rep. 150, 25 p.

TABLE 2.—Monthly captures and sex ratios of Jonah crabs caught with research traps, 1968-74. Asterisks denote significant deviation from 1:1 (chi-square).

Month	♂	♀	Ratio (♂:♀)	Month	♂	♀	Ratio (♂:♀)
Dec.-Apr.	10	4	2.5:1NS	Aug.	39	81	1:2.1**
May	7	3	2.3:1NS	Sept.	38	117	1:3.1**
June	8	2	4:1NS	Oct.	44	45	1:1NS
July	24	7	3.4:1*	Nov.	11	19	1:1.7NS

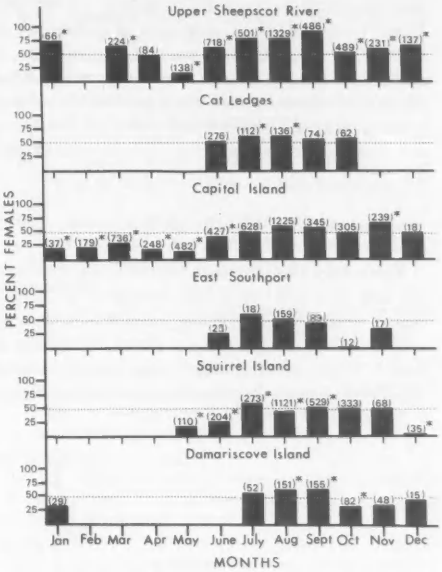
NS = not significant.
* = $P<0.05$.
** = $P<0.01$.

European edible crab have been reported to move inshore in spring and offshore in fall (Dewberry 1956; Hoopes 1973; Brown see footnote 3). In fact, mature female European edible crabs have been observed to move considerable distances (≥225 km) along the coast of England (Brown see footnote 3).

Sex ratios of rock crabs caught with research gear varied not only by season but also by area (Figure 7). From July through September females generally outnumbered males, throughout the fall many of the sex ratios approximated a 1:1 relation, and then in winter males were dominant except in the upper Sheepscot River where they predominated only in May. Similar to Jonah crabs, seasonal variations in rock crab sex ratios may best be explained by changes in the crabs' availability and vulnerability to the research traps in association with shedding and mating behavior. For instance, peak catches of females during summer and early fall coincided with egg hatching (summer) and molting (fall) in Maine waters (Krouse 1972).

Higher proportions of male rock crabs in winter and spring catches may be attributed to: 1) recruitment of males as the result of winter-spring shedding (Krouse 1972) and, possibly, inshore movement (Haefner [1976] suggested that male rock crabs in the Mid-Atlantic Bight undertake seasonal inshore-offshore migrations); 2) increased feeding activity of newly molted crabs; and 3) a reduction in the availability and vulnerability of females during the winter spawning period (Dewberry [1956] noted that ovigerous female *C. pagurus* consume little food). Throughout summer the number of male rock crabs, particularly those >90 mm CW, diminished due to fishing mortality and, perhaps, an offshore movement.

The upper Sheepscot River sites, unlike the other locations, had a preponderance of females during fall and winter, yet in spring, similar to other areas, males were more numerous (Figure 7). Perhaps this relatively high abundance of


Upper Sheepscot River
Cat Ledges
Capitol Island
East Southport
Squirrel Island
Damariscove Island
PERCENT FEMALES
100
75
50
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66 * 224 * (84) (138) (718) * (501) * (1329) * (486) * (489) * (231) * (137) *
(276) (112) * (136) * (74) (82)
(37) * (179) * (736) * (248) * (482) * (427) * (628) (1225) (345) (305) (239) * (18)
(18) (159) (63) (12) (17)
(73)
(110) * (204) * (273) * (1121) * (529) * (333) (68) (35) *
(29) (52) (151) * (155) * (82) * (48) (15)
Jan Feb Mar Apr May June July Aug Sept Oct Nov Dec
MONTHS

FIGURE 7.—Monthly percent frequencies of female rock crabs caught by research traps at different locations in the Boothbay region, 1968-74. Numbers in parentheses represent total number of males and females. Those ratios differing significantly from 1:1 ($P = 0.05$ by chi-square) are marked with asterisks. Blank bars represent no fishing effort.

females may be related to the Sheepscot River sites' soft mud substrate, which females apparently seek during the spawning season. From laboratory observations it appears that unless females are burrowed in the substrate at the time of egg extrusion, many eggs will not become attached to the pleopods resulting in a significantly reduced complement of eggs. Edwards and Early (1972) reported that female *C. pagurus* also show preference for soft substrates during the spring.

Lindsay (1973) also noted that sex ratios of Maine rock crabs vary by locality and season. He also found males to be more abundant in the winter and spring.

Width-Weight Relations

Because the overlap of data of males and females composed only a small segment of the total range of sizes, I applied analysis of covariance to the total regressions as well as the partial regressions derived from the data that

overlapped. Significant differences ($P = 0.05$) were found between the y-intercepts of either sex for both the complete and partial regressions, so males and females were treated separately. Plots of the predictive regressions show that male Jonah crabs averaged about 8% heavier than females of the same CW over the range 115-130 mm (Figure 8).

SUMMARY

From July 1968 through March 1978, 419 male (67-168 mm CW) and 535 female (74-136 mm) Jonah crabs were collected from research traps and commercial fishermen. Even though male Jonah crabs attain larger sizes (mean sample 113.7-141.1 mm CW) than females (mean sample 104.8-114.0 mm), many female Jonah crabs are harvested commercially whereas, rock crab landings are chiefly composed of males.

No Jonah crabs <67 mm CW were caught and only 2.7% of the total catch were <90 mm CW. This with other evidence indicates that small Jonah crabs inhabit greater depths (>20 m) than those sampled.

Catch per unit of effort values for Jonah crabs caught with research gear generally increased during summer, peaked in fall, and then declined sharply. Fluctuations in the catch were attributed primarily to movement. Catches were highest at the deeper, more seaward sampling sites where the substrate was predominantly rocky. In contrast, rock crabs were more abundant at those relatively shallow estuarine stations having soft

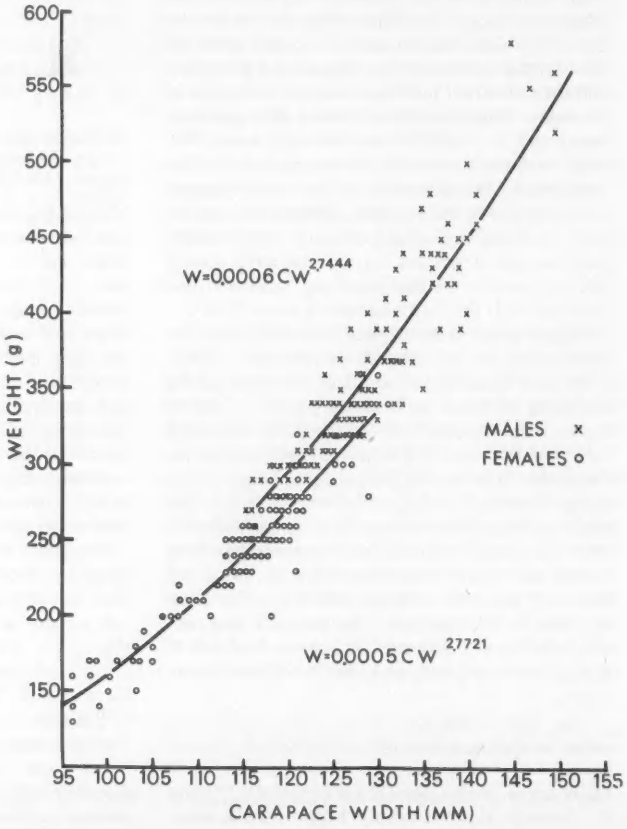

FIGURE 8.—Carapace width-weight relationships calculated for 110 male and 90 female Jonah crabs from the Boothbay Harbor region. Standard errors of the regression coefficients are 0.1793 (a) and 0.0850 (b) for males and 0.2023 (a) and 0.0984 (b) for females.

mud bottoms. Distribution of both cancrid crabs appears to be controlled by substrate type, depth, and temperature.

Male Jonah crabs outnumbered females in the catch in July; the opposite occured in August and September; during the remaining months, sex ratios did not differ significantly from 1:1. In comparison, female rock crabs generally predominated July through September, during fall most ratios approximated 1:1, and in winter and spring males usually dominated with the exception of most estuarine locations where males were only in the majority during May.

ACKNOWLEDGMENTS

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NOTES

EFFECTS OF DESICCATION AND AUTOSPASY ON EGG HATCHING SUCCESS IN STONE CRAB, *MENIPPE MERCENARIA*

The stone crab, *Menippe mercenaria*, is found from North Carolina to Yucatan, Mexico, Cuba, Jamaica, and the Bahamas; commercial fishing occurs principally in the State of Florida. Crabs are captured in wooden or plastic traps (40 × 40 × 28 cm) baited with available fish scraps. Present Florida laws allow harvest of both claws from all crabs, including ovigerous females, provided each claw is of legal size (70 mm propodus length). Sale of whole crabs is prohibited, and declawed crabs are released to allow regeneration of lost claws and renewal of fishable stocks. Regeneration of another legal claw can occur within 18 mo (Sullivan[1]).

The commercial season extends from 15 October to 15 May. Spawing occurs during the warmer months (Noe 1967; Cheung 1969), and females with large external egg masses (sponge) of up to 600,000 eggs are observed from early March to late November. Newly extruded eggs, attached to abdominal pleopods, are red-orange and progress to yellow then grey over a 9-12 day maturation period. Larvae generally hatch directly from eggs attached to pleopods. Most commercial operations maximize daily marketable claw yield by pulling traps continuously and declawing crabs only during the return trip to port. This necessitates keeping whole crabs in large fish boxes or containers on deck that are exposed to air for up to 8 h. Claw removal from air-exposed ovigerous females and desiccation of exposed egg masses may reduce larval hatching and recruitment. Since these procedures violate Florida law requiring crabs to be declawed immediately and released in the same area where captured, this study was conducted to provide scientific data to implement change in current fishing methods and protect future stocks.

Methods

Gravid stone crabs were captured in the Gulf of Mexico (5-9 m) west of Pass-A-Grille Beach, St. Petersburg, Fla., between March and September 1977. Females with large egg masses were transported in 4 l containers by ship to the Florida Department of Natural Resources Marine Research Laboratory. St. Petersburg. Container water, exchanged frequently with Gulf water while sampling, was not changed for approximately 1½ h during transport through low salinity waters.

Unfed crabs were kept individually in plywood tanks divided into compartments (45.7 × 30.5 × 30.5 cm), sealed with fiber glass tape and epoxy, and leached 2-4 wk prior to use. Water in the closed system was maintained at 15 cm depth by removable standpipes, and overflows were directed into individual glass tanks where eggs or larvae were retained before water entered two 1,000 l undergravel filter vaults (Dugan et al. 1975) (Figure 1). Overflow splash and two airlift standpipes maintained aeration.

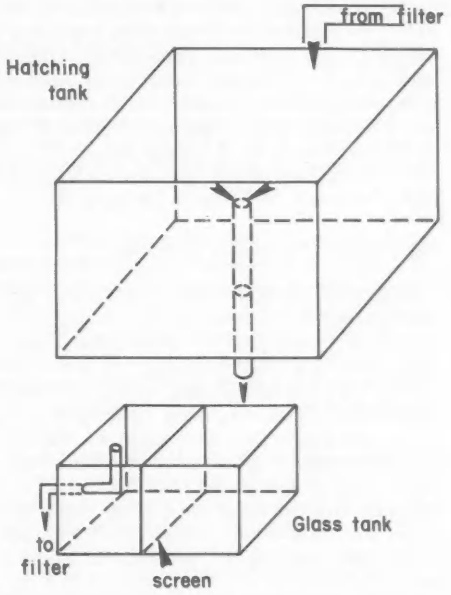

FIGURE 1.—Hatching tank (45.7 × 30.5 × 30.5 cm) and glass larval capture tank (15 × 15 × 30 cm) for desiccation and autospasy experiments with ovigerous stone crabs.

[1]J. R. Sullivan, Florida Department of Natural Resources, Marine Research Laboratory, pers. commun. May 1977.

Optimum survival conditions for egg development and hatching success for *M. mercenaria* (30° C and 34‰ salinity) were determined by Ong and Costlow (1970). Salinity in the present study varied between 32.0 and 36.0‰ and averaged 34.4‰ in all experiments. Air and water temperatures in the control room fluctuated from 27° to 33° C with water temperature generally 0.5°-1.0° C lower. Dissolved oxygen levels were measured twice monthly. Nitrites and ammonia levels were evaluated weekly and never exceeded 0.089 and 0.073‰, respectively. Lighting was regulated for 16 h light: 8 h dark and utilized Vita-Lite[2] bulbs which simulated the natural spectrum of sunlight (Dugan et al. 1975).

Experiment I (13 April-31 July)

Crabs were divided into three test groups, with similar ranges of animal size and egg mass color (maturity) and were acclimated to tanks for at least 18 h. Initially, individual crabs were exposed to ambient indoor air conditions in separate cages. This procedure was modified after the first series to simulate commercial holding techniques more closely by placing crabs from a single group into loosely covered wooden slat boxes located in direct sunlight. After desiccation, crabs were returned to holding tanks and observed every 24 h until all eggs hatched. Group I (control) crabs remained in water throughout the experiment. Group II and Group III crabs were desiccated for 2 and 5 h, respectively. Total number of crabs for each group was: 35-Group I, 34-Group II, 33-Group III.

Experiment II (5 August-21 September)

Desiccation procedures were identical to modified procedures in Experiment I; added stress from claw removal was introduced after desiccation. Claws were removed using commercial harvesting methods by inducing autospasy (loss of appendage through externally applied pressure). In this technique, claws were grasped firmly and ventral pressure applied until the fused basischium stopped against the coxa. Further flexion strained the autotomizer muscle, and separation of the limb occurred at a natural fracture plane. Excessive hemorrhaging is prevented by swelling of a hypodermal diaphragm located at the fracture plane.

Group IV (control) crabs remained in water throughout the experiment and had similar treatment as Group I. Group V and Group VI crabs were desiccated for 2 and 5 h, respectively, then declawed. Declawed crabs were placed immediatedly into holding tanks and observed every 24 h as in Experiment I. Total number of crabs for each group was: 30-Group IV: 34-Group V; and 35-Group VI.

Crabs continuously discarded eggs from egg masses. Single eggs were shed when females raised their bodies on claws and legs and preened (combed) egg masses with rear legs. Egg stalks containing up to several hundred eggs (clumps) were also frequently shed. Aeration of eggs by rapid abdominal movement also occurred at this time. Detached eggs, larvae, and other egg mass products retained in individual glass tanks were removed daily and preserved in 10% Formalin prior to counting.

Analysis

Hatching occurred from 0 to 9 days after day of experimental stress. Complete hatching generally required 24-48 h, and organic matter retained in glass tanks after that time was principally dead eggs, deformed larvae, or empty egg cases cleaned from pleopods.

The day with highest number of normal first-stage larvae was called major hatch. Days before and following major hatch were called prehatch and posthatch.

Eggs from a single ovigerous female were observed microscopically to determine normal hatching process and identify normal first-stage larvae. Initial breaking of the chorion enabled larvae to emerge head first from the egg. Vigorous abdominal flexing by the larvae cast off the egg case and induced shedding of the prezoeal cuticle and full extension of the rostral and lateral spines. In a few instances, spinular extension was delayed until complete seperation from the egg, but all prezoea yielded normal, active free-swimming first-stage larvae within minutes of initial hatch. Eggs removed from the same female after desiccation were observed for comparison. Increased numbers of inviable eggs and partial hatches were evident. Numerous prezoea, unable to cast off prezoeal cuticles, died after continued struggle. Successful first-stage development was reduced, and

[2]Reference to trade names does not imply endorsement by the Marine Research Laboratory, FDNR or the National Marine Fisheries Service, NOAA.

larval activity was sluggish, frequently ending in death.

Aliquots from individual daily crab samples (1 or 2 ml; count ≃ 200) were sorted under a dissecting microscope and classified. Normal first-stage larvae (Hyman 1925; Porter 1960) were denoted as viable; whole eggs, partially hatched eggs, prezoea (Hyman 1925; no rostral or lateral extension), and deformed first-stage larvae were denoted as inviable. Stein's two-stage sample test (Steel and Torrie 1960) indicated that six replicate aliquots from each sample provided reliable counts (within 95% confidence limits) of total numbers of viable and inviable eggs and larvae present each day. Because results of aliquot counts were inconsistent when samples contained clumps of eggs, 1-8 ml of chlorine bleach (5.25% sodium hypochlorite) were added to dissolve stalks and dissociate eggs uniformly before aliquots were taken.

Number of eggs carried by individual crabs at time of capture was estimated by combining daily totals of viable and inviable eggs and larvae. Total hatching success was expressed as percent of original egg mass that hatched viably. Total egg mass mortality was expressed as the percent not hatching or hatching inviably. Average daily mortality (per group) was calculated by dividing total mortality per day by the number of crabs yielding inviable eggs and larvae that day. Crabs not yielding any larvae were eliminated from analysis; two crabs in Group I and one crab each in Groups III, IV, and VI were so eliminated.

Comparison among groups was made by presenting prehatch, posthatch, and total egg mass mortality for each group. I chose this method because inviable eggs and larvae were evident in some form in all daily samples, but viable larvae were present for only 24-48 h.

Results and Discussion

Experiment I

Initial egg loss from crabs in Group I (Figure 2) was probably caused by handling at capture and stress from transport to laboratory. With acclimation to holding tanks, average daily mortality decreased until major hatch, when highest egg and larval mortality coincided with maximum first-stage larval survival.

Crabs desiccated for 2 h (Group II) showed immediate preening activity upon return to water and daily prehatch mortality peaked at 3.6%, 3 days after desiccation (Figure 2). Thereafter, daily percent mortality decreased until major hatch. Posthatch mortality was similar to, but slightly higher than that of Group I. Total prehatch mortality (12.1%) was four times greater than that of Group I (Table 1) and posthatch mortality (9.3%) was nearly twice that of Group I. Total mortality for Group II (21.4%) was 13.0% higher than control (Group I).

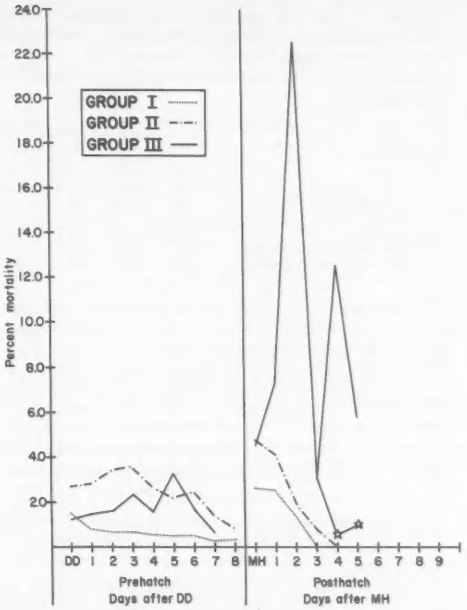

FIGURE 2.—Average daily percent egg mortality in ovigerous stone crabs as related to desiccation. Group I crabs untreated (control), Group II crabs exposed to 2-h desiccation and Group III crabs exposed to 5-h desiccation. DD - day of desiccation; MH - day when major hatching occurred; Prehatch - days following DD; Posthatch - days following MH. Starred points represent percent mortality excluding one of three crabs which accounted for 96% total mortality on posthatch days 4 and 5.

Desiccation for 5 h (Group III) caused temporary lethargy in crab mobility; sponge care and initial mortality were below those of Group I (Figure 2). Crabs recovered slowly during prehatch, resulting in 5 days of generally increasing daily egg mortality. Maximum daily egg and larval mortality usually occurred on the day of major hatch, but was delayed 2 days for most Group III crabs. Improper maternal care of eggs during prehatch and through posthatch may have prolonged oxygen

TABLE 1.—Percent egg mortality in ovigerous stone crabs as related to desiccation and autospasy. Experiment I compares egg mortality after effects of desiccation and experiment II compares egg mortality after desiccation followed by removal of both claws (autospasy).

Group and treatment	Crabs (no.)	Prehatch	Posthatch	Total
Experiment I:				
I (control)	33	3.3	5.1	8.4
II (2-h desiccation)	34	12.1	9.3	21.4
III (5-h desiccation)	32	5.9	33.8	39.7
Experiment II:				
IV (control)	29	7.0	6.7	13.7
V (2-h desiccation/autospasy)	23	8.5	18.1	26.6
VI (5-h desiccation/autospasy)	16	9.8	50.4	60.2

deficiency within the egg mass and lack of abdominal movement may have hindered successful larval hatching. Davis (1965) separated eggs from female blue crab, *Callinectes sapidus*, and noted a decrease in hatching success if eggs remained in small clusters, presumably due to insufficient oxygen. Rice and Williamson (1970) found that decapod larvae hatched from ovigerous females were weakened if oxygenated water could not be replenished.

Prehatch mortality for Group III (5.9%) was less than that of Group II, but was still greater than that of Group I (Table 1). Posthatch mortality (33.8%) was considerably higher than Group I or Group II. Total mortality for Group III (39.7%) represented a mean increase of 18.3% mortality above that of Group II and a mean increase of 31.3% above that of Group I (Table 1).

Experiment II

Autotomizer muscle reflexes were adversely affected in crabs subjected to air exposure, and declawing often resulted in jagged wounds and severance of the artery proximal to the hypodermal diaphragm. Unrestricted hemorrhaging caused death in 8 crabs in Group V and 14 crabs in Group VI. Death in seven additional crabs (three in Group V, four in Group VI) could not be explained as above, but also occurred after declawing. Resulting 100% egg mass mortality for 34.4% of Group V and 52.9% of Group VI notably reduced group mean hatching success related to control Group IV (Table 1).

Wood and Wood (1932) found any treatment which weakened brachyurans affected muscular responses, preventing normal autotomic reflex; they further stated that American crayfish (Astacidae) held captive for any length of time were vitiated and lacked normal reflex. Davis[3] related wound size and body fluid loss in reporting 53.7% death in *M. mercenaria* held for 10 days in laboratory tanks and then declawed using commercial methods.

Loss of both claws after desiccation reduced preening of eggs by surviving crabs, resulting in an apparent initial egg mass mortality below that of Group IV (Figure 3).

Group V crabs (2-h desiccation) recovered quickly and compensated for claw loss by propping themselves against sides of compartments; rocks and shells common where stone crabs occur may be used similarly in nature. Prehatch mortality peaked 3 days after desiccation. Posthatch mortality was higher and more erratic than that of control Group IV. Prehatch mortality (8.5%) was slightly higher than that of Group IV (7.0%), but posthatch mortality (18.1%) was almost three times higher than that of control group (Table 1). Total mortality for Group V (26.6%) was 12.9% above control (Group IV).

[3]Davis, G. E. Interim report June, 1977. National Park Service Stone Crab Study. Everglades National Park, Box 279, Homestead, FL 33030.

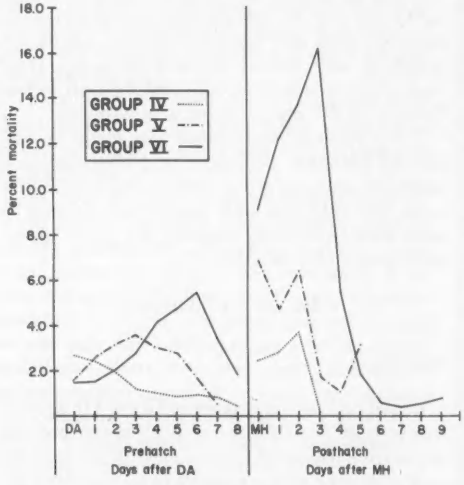

FIGURE 3.—Average daily percent egg mortality in ovigerous stone crabs as related to desiccation and autospasy. Group IV crabs were untreated (control), Group V crabs had both claws removed (autospasy) after 2-h desiccation, and Group VI crabs had both claws removed after 5-h desiccation. DA - day of desiccation and autospasy; MH - day when major hatching occurred; Prehatch - days following DA; Posthatch - days following MH.

After 5-h desiccation, surviving declawed crabs (Group VI) recovered more slowly than did crabs of Group V. Maternal preening was delayed and egg mortality during prehatch did not peak until 6 days after desiccation (Figure 3). As noted previously, maximum egg and larval mortality normally occurred at major hatch, but difficulty in maintaining body elevation probably inhibited preening for Group VI during posthatch. Consequently, maximum egg and larval mortality occurred 3 days after major hatch and time needed to clean pleopods was extended to 9 days.

Group VI recovery from stress was sufficient to produce prehatch mortality of 9.8%, an increase of 2.8% above control Group IV (Table 1). Extended posthatch yielded 50.4% egg and larval mortality, the highest of any group. Total mortality for surviving crabs in Group VI (60.2%) was a marked increase of 46.5% above that of control Group IV (Table 1) even excluding 100% mortality values from 18 dead crabs.

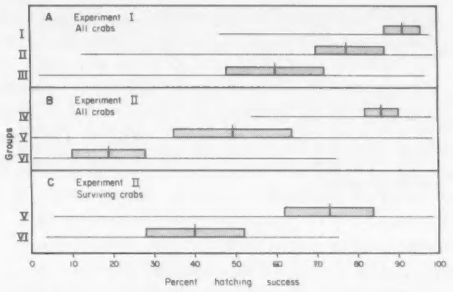

FIGURE 4.—Hatching success in ovigerous stone crabs as related to desiccation and autospasy. Mean (vertical line), range (horizontal line) and 95% confidence intervals (bar) about the mean. Set A includes untreated Group I crabs, Group II crabs exposed to 2-h desiccation and Group III crabs exposed to 5-h desiccation; Set B includes untreated Group IV crabs, Group V crabs, both claws removed after 2-h desiccation and Group VI crabs, both claws removed after 5-h desiccation; Set C includes only crabs that survived desiccation and autospasy in Groups V and VI.

Mean Hatching Success

Mean hatching success for control crabs in Experiment I (Group I) was 91.6%. Desiccation from air exposure for 2 h (Group II) decreased success to 78.6% and desiccation from 5-h air exposure (Group III) decreased success to 60.3%. Mean hatching success for control crabs in Experiment II (Group IV) was 86.3%. Stress from 2-h desiccation plus autospasy (Group V) decreased success from Group IV to 49.6% and stress form 5-h desiccation plus autospasy (Group VI) decreased success to 18.8% (Figure 4).

Summary

Desiccation of eggs by air exposure of ovigerous females caused reduction in larval hatching success that was directly related to length of exposure. Desiccation weakened normal crab autotomic muscular reflex, and experimental declawing resulted in death of 34.4% of crabs exposed 2 h and 52.9% of crabs exposed 5 h.

Stress from autospasy after 2-h desiccation did not increase mean egg and larval mortality for surviving crabs above that for crabs desiccated only. Related to controls, Group II (2-h desiccation) and Group V (2-h desiccation/autospasy) had nearly identical total mortalities, 12.9% and 13.0%, respectively. Claw loss delayed maternal egg mass preening, and reversed the prehatch/posthatch egg mortality ratio of crabs desiccated 2 h from 12.1:9.3 (Group II) to 8.5:18.1 (Group V).

Effects of stress after 5-h air exposure were less definitive. Egg and larval mortality for surviving declawed crabs exposed to 5-h desiccation was 15.5% higher than was mortality for similarly exposed whole crabs when related to controls. Maternal egg preening by declawed crabs was obviously affected by claw loss, but small sample size (16) in surviving declawed crabs and overlap in confidence intervals for the 5-h desiccation groups made differences in mortalities inconclusive.

The stone crab fishery, unlike the blue crab fishery which allows permanent removal of whole animals, realizes high stability and recruitment by release of reproductively active crabs capable of claw regeneration. Present harvesting techniques adversely affect this stability by subjecting crabs to air exposure and desiccation. When crabs are ovigerous, desiccation causes a definite reduction in larval hatching success and is related to crab death and reduced overall population recruitment. Protection of ovigerous females by immediate release or by use of methods to dampen crabs while on deck is therefore warranted.

Acknowledgments

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FIRST RECORDS OFF OREGON OF THE PELAGIC FISHES *PARALEPIS ATLANTICA*, *GONOSTOMA ATLANTICUM*, AND *APHANOPUS CARBO*, WITH NOTES ON THE ANATOMY OF *APHANOPUS CARBO*[1]

The species covered in this report are common in parts of the Atlantic Ocean and all are known to occur in the Pacific Ocean. We fill a gap in knowledge of the distribution of two species known formerly only north and south of Oregon, extend the northward range of *Gonostoma atlanticum* Norman, and report inshore occurrences of *Paralepis atlantica* Krøyer. The unusual gross anatomy surrounding the gas bladder of *Aphanopus carbo* Lowe is worthy of description.

Methods

Counts and measurements followed those of Hubbs and Lagler (1958) and all measurements were taken to the nearest 0.1 mm. Specimens are catalogued in the fish collections of the Department of Fisheries and Wildlife (OS) or the School of Oceanography (OSUO), Oregon State University. Anatomical terminology follows that of Lagger et al. (1962) and Romer (1970). Four specimens of *A. carbo* from Oregon were dissected and two were radiographed. Two specimens from the Atlantic Ocean off Madeira were dissected and radiographed. Complete vertebral counts could not be made from the radiographs due to poor resolution of the small posterior caudal vertebrae.

Notes on Distribution and Morphology

Paralepis atlantica has been recorded in the eastern Pacific from Baja California and California (Rofen 1966) and from the vicinity of Willapa Bay, Wash. (Kajimura 1969). Bakkala (1971) reported the species from surface waters of the central Pacific at lat. 48°00′ N, long. 165°00′ W.

Two specimens of *P. atlantica* were found on shore in northwestern Oregon. One (OS 956:456 mm SL) was taken alive on the beach at Netarts, Tillamook County, on 7 October 1963. Another (OS 5160:466 mm SL) was found dead on the beach 29 km north of Seaside, Clatsop County, on 16 May 1960. A specimen of *G. atlanticum* (OSUO 2402:59 mm SL) was captured on 30 July 1977, 65

[1]Technical Paper No. 5082, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, OR 97331.

km west of Newport (lat. 44°38′ N), between 335 and 400 m deep with a small Cobb midwater trawl (10 m mouth opening) with an opening and closing cod end (Pearcy et al. 1977). This female fits the descriptions by Grey (1960, 1961, 1964) and Mukhacheva (1972). Maximum diameter of eggs in the ovary was 0.16 mm. Grey (1964) considered fish of this size to be mature.

Gonostoma atlanticum is usually distributed in warm water of the Atlantic, Pacific, and Indian Oceans. It is found in the eastern and central North Atlantic, and it has usually been recorded from equatorial waters in the Pacific and Indian Oceans. The northernmost previous record (lat. 34°18.6′ N) for its occurrence in the Pacific Ocean was that of Berry and Perkins (1966), who captured several individuals off southern California. The temperature of the water in which the OSUO specimen was captured was 5.37°-5.70° C. Backus et al. (1965) reported the occurrence of *G. atlanticum* in the Atlantic Ocean in waters of 10°-11° C.

Aphanopus carbo was first reported from the Pacific Ocean off Bodega Bay and Fort Bragg, Calif., in 1969 (Fitch and Gotshall 1972). Peden (1974) reported a specimen from off the Strait of Juan de Fuca. Clarke and Wagner (1976) collected larvae and juveniles off Hawaii. Five specimens were taken off Oregon in 1976: OS 5381 (476 mm SL), about 29 km off Cape Meares, at about 183 m; OS 6115 (639 mm SL), about 37 km off Florence, at about 146 m; OSUO 2352 (570 mm SL), 2353 (558 mm SL), 2354 (547 mm SL), 120 km west of Newport, at about 400-480 m, in an opening and closing net.

Our specimens compared with those from Madeira, had slightly smaller horizontal orbit, slightly wider suborbital head width, and slightly shorter anal spines. Otherwise the Atlantic and Pacific Ocean specimens are very similar.

Gas Bladder Anatomy in *Aphanopus carbo*

Although Maul (1954) mentioned that on retrieval to the surface the gas bladder in *A. carbo* expands greatly, causing the skin of the abdomen to split, none of our specimens exhibited this characteristic. Shepel[2] stated that none of the specimens examined by him had their skin split, but that the stomach in most specimens (all from the Atlantic Ocean) were everted. Only one of our specimens had an everted stomach. These differences led us to examine the gas bladder and associated structures in *A. carbo*.

Bone (1971) described the anatomy and histology of the gas bladder of *A. carbo*. Tucker (1953) briefly mentioned the ribs and provided partial radiographs of the ribs and vertebral column in *A. carbo* and *A. schmidti*. However, we found no descriptions of the relationship of the bladder to the vertebral column, ribs, kidneys, and coelom. Our examination of *A. carbo* shows that the gas bladder of this species, and the structures associated with it, has several unusual characteristics. Little variation in anatomy was noted in our specimens.

The position of the gas bladder in *A. carbo* is typical of that in most fishes; it is ventral to the vertebral column and kidneys and dorsal to the peritoneal (abdominal) cavity (i.e., retroperitoneal) (Figure 1). The anterior end of the gas bladder is below the sixth vertebra. From it, two minute extensions proceed anterolaterally at 45°, but the size of the extensions did not allow us to trace them forward more than a few millimeters. Posteriorly, the gas bladder extends to a blunt end between vertebrae 42 and 45, directly dorsal or slightly anterior to the vent. Although the dorsoposteriad portion of the peritoneal cavity narrows and curves ventrally, the gas bladder continues to parallel the vertebral column except for a slight dip near the posterior end. The region between the gas bladder and the peritoneal cavity is filled with hypaxial muscle. The bladder is slightly narrowed at its anterior and posterior ends. It is oval in cross section and slightly smaller than the diameter of vertebral centra in our preserved specimens (Figure 1).

The kidneys extend anteriorly from the region dorsal to the vent to the posterior portion of the skull. They are enlarged in the area above the vent, and between the anterior of the gas bladder and posterior of the skull, and lie ventrolateral to the vertebral column and dorsolateral to the gas bladder. They terminate in a urinary duct that appears to empty into a urogenital sinus.

The ventral ribs are intimately associated with the gas bladder and kidneys. A pair of ventral ribs is present on all trunk vertebrae, but those anterior to the gas bladder are short and thin. These ribs are difficult to find but may be seen readily in radiographs. From immediately anterior to the gas bladder to about the ninth vertebra the ribs become progressively longer and

[2]L. I. Shepel, Fishery Reconnaissance, Murmansk, U.S.S.R., pers. commun. 15 November 1977.

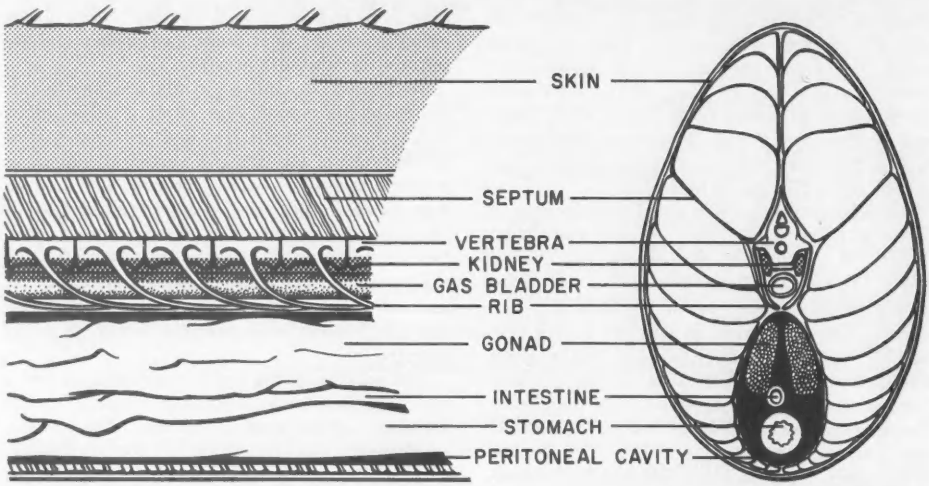

FIGURE 1.—Gross anatomy of the gas bladder and surrounding region in the black scabbardfish, *Aphanopus carbo*. Left: Partial sagittal section in region of the 14th-19th vertebrae. Muscle and other tissue have been removed from the region ventral to the indicated septum. Right: Cross section in the region of the 14th vertebra.

thicker. From that point posteriorly to the first caudal vertebra, all the ribs, except the last two to four, are of the same size, shape, and relative position. All the ribs extend laterally around the kidneys but the last few extend farther ventrally to encage the enlarged posterior portion of the kidneys. Where the ribs contact the gas bladder laterally, they turn abruptly posteriad and almost parallel the bladder while remaining in contact with it. In doing so, they curl beneath the bladder. Each rib extends posteriorly a distance almost equal to two vertebrae (Figure 1). Each rib appears to join a myocomma, then connect to the ventrolateral wall of the bladder. The gas bladder is thus surrounded by a "rib cage."

The hypaxial muscles, in conjunction with the ribs, surround the gas bladder almost completely. The only gap is a narrow medial band of connective tissue to which the ribs attach, present between the peritoneal membrane and the gas bladder (Figure 1).

The unusual anatomy of *A. carbo* invites speculation concerning its significance. The enclosure of the gas bladder in a rib cage apparently reinforces the gas bladder wall, which Bone (1971) has shown is composed of thick connective tissue. The combination of a thick, tough wall reinforced by muscle and bone seems likely to prevent the expansion of the gas bladder when ambient pressure decreases more rapidly than the gas contained in the bladder can be absorbed into the bloodstream. This species is known to feed on cephalopods (Zilanov and Shepel 1975). Possibly the anatomical modifications of its gas bladder and associated structures allow *A. carbo* individuals to pursue prey into significantly shallower water without having to adjust bouyancy and/or absorb gas.

Acknowledgments

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CHANGES IN RIBONUCLEIC ACID, DEOXYRIBONUCLEIC ACID, AND PROTEIN CONTENT DURING ONTOGENESIS IN WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*, AND EFFECT OF STARVATION

Normal development of most embryonic and prolarval (yolk-sac) teleosts depends on material stored in the yolk for a source of both energy and biosynthetic precursers. After hatching there is a transition period when larvae shift from dependence on yolk to an exogenous food supply. The availability of sufficient prey of the proper quality and the ability of larvae to capture and assimilate it are critical to survival during the larval stage. Since differential mortality during the larval stage could be important in determining the year-class size of marine fish, a method for determining the nutritional condition of fish larvae in plankton samples could aid in determining larval survival and prediction of subsequent year-class size. In the past, weight-length relationships (Blaxter 1971), morphometric (Ehrlich et al. 1976), chemical (Ehrlich 1974a, b), and histological (O'Connell 1976; Theilacker 1978) methods have been used with varying degrees of success. All four approaches have limitations and diagnosis of the starving condition in sea-caught larvae is difficult.

Bulow (1970) used RNA-DNA (ribonucleic acid-deoxyribonucleic acid) ratios as indicators

of recent growth rates in golden shiner, *Notemigonus crysoleucas*, adults. He reported that RNA-DNA ratios were very sensitive to changes in feeding levels. The RNA content of a wide variety of organisms have been related to growth rate (Sutcliffe 1970). Sutcliffe (1965) was able to predict quite accurately the growth rates of laboratory populations of brine shrimp, *Artemia salina*, and mud snail, *Nassarius obsoletus*, larvae using a growth-RNA relation determined on whole amphipod *Orchestia platesis*. Dagg and Littlepage (1972), however, concluded that the general positive relationship between growth rate and RNA content lacked sufficient specificity for determination of growth rate. A positive relationship is expected since growth in marine teleosts is accompanied by and is partially a function of protein synthesis, and certain types of RNA are directly involved in protein synthesis serving as both a template and organizer. The DNA content of an organism has been used as an indication of cell number since the DNA content of somatic cells is generally constant for a given species. Some eggs and early larvae, however, have been shown to contain large amounts of cytoplasmic DNA, greatly exceeding the amount of nuclear DNA (Neyfakh and Abramova 1974). This study was undertaken to determine the relationships between changes in DNA, RNA, and protein content and events in the development of winter flounder, *Pseudopleuronectes americanus*, and to determine if measurements of these classes of biochemicals could be used to determine the nutritional condition of winter flounder larvae.

Methods

Pseudopleuronectes americanus adults were caught by trawl net off Rhode Island and kept in a 1,900 l aquarium. Eggs were obtained, fertilized, and incubated according to methods previously described (Smigielski 1975). Larvae were maintained at 8° C in 38 l all black glass aquaria. Commencing 4 days after hatching the larvae were fed zooplankton collected in the Narragansett Bay area in excess of 2 organisms/ml according to the methods of Laurence (1975). On days 3 and 28 a portion of the larvae were transferred to an identical aquarium containing seawater filtered through a 0.45 μm Millipore[1] filter. Wild winter flounder larvae were collected in Narrow River, R. I., with a 505 μm 0.5 m plankton net.

About 40 eggs or larvae were pooled per sample through day 11 after hatching; thereafter 10 larvae were pooled per sample except on days 43, 50, and 58 when only 5 larvae were used for the largest size group. All samples through day 36 were run in triplicate; thereafter samples were run in duplicate. Starting on day 28 the standard length of each larva sampled was determined using an ocular micrometer and 10 larvae were taken on each sampling day for dry weight determinations.

Eggs and larvae were homogenized in 2 ml of ice-cold distilled water immediately after sampling. Protein was determined on duplicate 0.1 or 0.05 ml samples of homogenate using a modification of the Lowry method (Hartree 1972). RNA and DNA were extracted and partially purified from 1.7 ml of homogenate using a modification of the Schmidt-Thannhauser method (Munro and Fleck 1966) adapted for the micro quantities present in larval fish and eggs. RNA concentration was estimated from the absorbancy at 260 nm of the acid-soluble, alkali-hydrolyzed fraction. The DNA content of larvae was determined from the absorbency at 260 nm of the alkali-stable, acid-hydrolyzed fraction. Because of the very small quantities of DNA in winter flounder eggs their DNA content was determined on the alkali-stable fraction using a modification of the 3,5-diaminobenzoic acid dihydrochloride florometric assay described by Holm-Hansen et al. (1968) and Hinegardner (1971). At the beginning of this study RNA was also determined using the orcinol method (Sutcliffe 1965) and DNA was determined using the indole method (Ceriotti 1952). These values were in good agreement with the values reported.

Results

DNA content per egg increased rapidly between fertilization and hatching (Figure 1). Upon hatching 10 days after fertilization, larvae contained slightly more RNA and DNA than unhatched eggs and retained 78% of the protein. During the period from hatching to the end of the yolk-sac stage (day 5), DNA and RNA content remained essentially constant while a decrease in protein was observed. Although plankton was added on day 4 to aquaria containing fed larvae, visual observation of the gut indicated that the majority of the larvae had

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

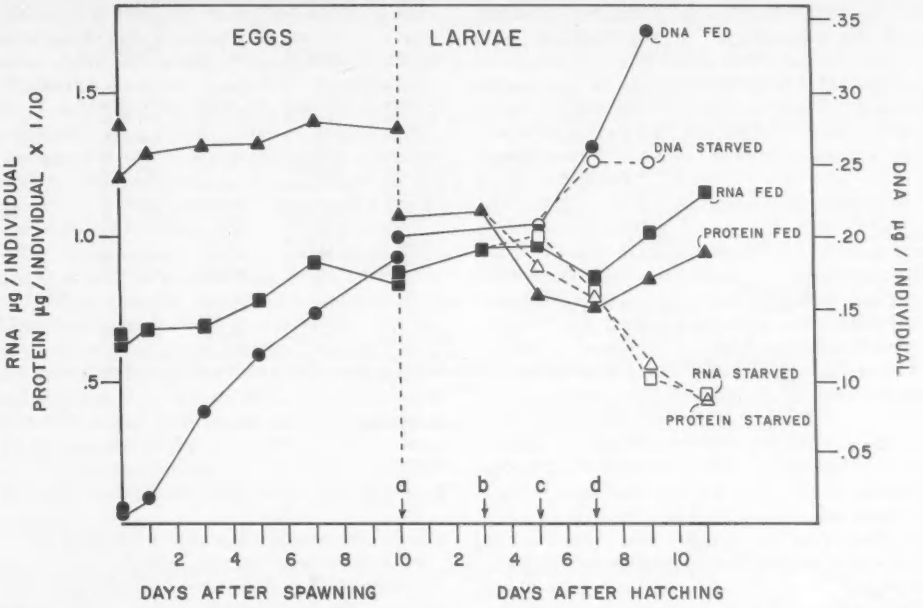

FIGURE 1.—Time course of development of DNA, RNA, and protein content per individual winter flounder egg or larva. a) 50% hatch; b) starved larvae transferred to filtered seawater; c) most larvae showed no visible yolk; d) food visible in gut of fed larvae.

not begun feeding until day 7. Between the end of the yolk-sac stage and initiation of feeding (day 7) DNA content increased sharply while RNA and protein decreased. Of the protein present in the egg just prior to hatching, 45% was lost by the time of feeding initiation. After feeding initiation DNA, RNA, and protein content increased steadily (Figure 1; Tables 1, 2).

The RNA and protein content of winter flounder larvae transferred to filtered seawater prior to feeding initiation continued to decrease until a 100% mortality was observed between day 11 and 14 (Figure 1). Starved larvae did show an increase in DNA content on day 7 similar to that observed in fed larvae. The RNA-DNA ratio of both starved and fed larvae decreased from the end of the yolk-sac stage through day 9. However, the RNA-DNA ratio was significantly higher in fed larvae than starved larvae on day 9.

The RNA content of a second group of larvae transferred to filtered seawater 28 days after hatching decreased within 2 days, while both DNA and protein content appeared to increase (Table 1). After 4 days a decrease in all three components was observed. A 50% mortality, consisting almost entirely of the smaller individuals

TABLE 1.—RNA, DNA, and protein content of starved and fed winter flounder larvae 28 to 36 days after hatching.

Age (days)	Starvation time[1] (days)	Standard length[2] (mm)		RNA[3] (µg/larva)		DNA[3] (µg/larva)		Protein[3] (µg/larva)		RNA/DNA[3]	
		Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved	Fed	Starved
28	0	5.61±0.60		3.85±0.67		0.91±0.21		36±7		4.27±0.42	
30	2	5.83±0.72	5.64±0.56	4.74±0.73	3.32±0.51	0.99±0.13	1.04±0.11	37± 3	44±5	4.81±0.56	3.16±0.26
32	4	5.84±0.66	5.68±0.54	4.75±0.14	2.59±0.61	1.21±0.16	0.93±0.13	79± 4	36±7	3.99±0.50	2.78±0.29
	C[4]	5.44±0.80		3.95±0.22		0.99±0.05		43± 4		3.98±0.06	
36	8	6.53±0.92	6.41±0.45	8.91±0.66	3.70±0.50	2.17±0.41	1.73±0.18	94± 4	60±8	4.19±0.43	2.14±0.16
	C[4]	6.23±0.94		8.15±2.67		1.92±0.46		86±24		4.20±0.34	

[1]Number of days starved fish were in filtered seawater.
[2]Data are means ±1 SD for 40 to 50 larvae.
[3]Data are means ±1 SD of three replicates containing 10 larvae each.
[4]Fish removed from fed population and transferred to filtered seawater 18 h prior to sampling to clear stomach contents.

TABLE 2.—RNA, DNA, and protein content of wild and cultured (fed) winter flounder.

Age (days after hatching)	Standard length (mm) Range	Mean	SD	RNA (μg/larva)	DNA (μg/larva)	Protein (μg/larva)	RNA/DNA
Cultured larvae[1]:							
42	4.98–6.07	5.60	0.39	3.55±0.23	—	44± 1	—
	6.27–6.89	6.50	.20	9.19±0.75	1.99±0.06	99±10	4.61±0.09
	7.00–8.77	7.77	.57	21.83±1.98	3.91±0.70	200±15	5.62±0.52
43	5.26–6.35	5.76	.30	3.35±0.61	0.82±0.13	44± 5	4.10±0.07
	6.36–7.26	6.82	.26	7.75±0.98	1.85±0.25	91± 5	4.18±0.03
	7.29–8.54	8.19	.33	27.42±0.28	4.84±0.00	274± 5	5.67±0.06
50	4.10–6.54	6.01	.55	5.32±0.40	1.27±0.08	49± 4	4.19±0.03
	6.31–7.69	7.00	.34	11.08±0.29	2.52±0.02	115± 1	4.40±0.08
	[2]7.50–8.67	8.83	.56	32.82±2.83	6.19±0.69	370±37	5.31±0.14
58	5.79–6.91	6.31	.27	5.70±0.03	1.35±0.07	64± 1	4.23±0.20
	6.67–8.35	7.27	.47	14.33±1.03	3.18±0.08	153± 1	4.50±0.21
	[3]7.40–8.49	7.33	.31	37.08±1.02	7.05±0.10	434± 3	5.26±0.07
Wild larvae[4]:							
Group I	7.29–7.45	7.34	.09	19.05	4.19	212	4.55
II	5.80–6.71	6.41	.53	—	2.48	131	—
III	6.54–7.54	6.95	.41	25.36±3.20	5.45±0.34	376±43	4.65±0.41

[1]Standard length data for cultured larvae are means ±1 SD for 50 to 150 larvae. Chemical data are for two replicates consisting of 10 larvae each except for the largest size group on days 43, 50, and 58 when only 5 larvae were used per replicate.
[2]In this sample, 6 of the 10 fish had metamorphosed.
[3]In this sample, all fish had metamorphosed.
[4]Data for Groups I and II represent values for pools of three larvae each. Data for Group III are means ±1 SD for five larvae analyzed individually.

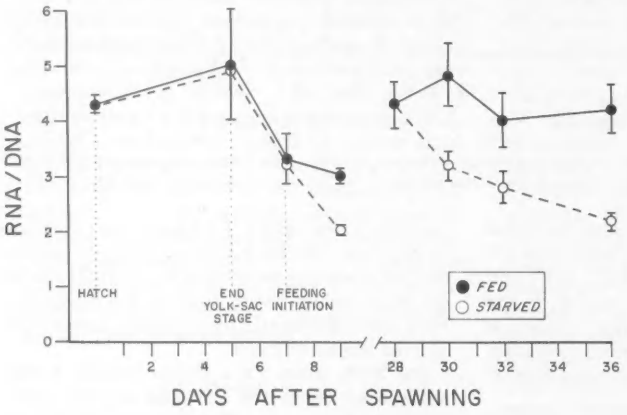

FIGURE 2.—RNA-DNA ratios of starved and fed winter flounder larvae. Open circles indicate values for larvae transferred to filtered seawater on day 3 and day 28. Brackets indicate ±1 SD.

in the group, occurred 7 days after transfer to filtered seawater, accounting for the high DNA, RNA, and protein values observed on the final day of sampling (day 36). The RNA-DNA ratio of larvae transferred to filtered seawater decreased continually until a 100% mortality was observed. No significant change in the RNA-DNA ratio of fed larvae was observed during the same period (Figure 2). The DNA, RNA, and protein content of different size groups of wild and cultured larvae through metamorphosis is shown in Table 2.

Discussion

The DNA, RNA, and protein content of winter flounder eggs reported in this study are total values for the yolk plus the embryo. Any increase in the amount of a particular component must therefore result from synthesis rather than transfer from the yolk to the embryo. The continual net accumulation of DNA from fertilization to hatching is probably correlated with an increase in cell number (Regnault and Luquet 1974) although the content of DNA per cell may decrease (Neyfakh and Abramova 1974). The small increase in protein content during the same period is evidence that protein is not an important energy source during early development in winter flounder. The 46% decrease in protein content between the maximum 3 days prior to hatching and the

minimum at initiation of feeding on day 7 indicates that protein is probably an important energy source during this period although this includes a 22% decrease in protein upon hatching, the majority of which may be lost with the chorion. Two periods of decrease in RNA content were observed. One occurred just prior to hatching; the other just prior to feeding initiation. No significant net decrease in the DNA content of eggs or fed larvae was observed between any sampling periods.

The decrease in protein and RNA content (Figure 1) as well as the decrease in the RNA-DNA ratio (Figure 2) prior to feeding initiation resembles the pattern observed for starved larvae. Even in the presence of excess food the RNA-DNA ratio fell from 4.9 at the end of the yolk-sac stage to 3.0 at initiation of feeding on day 7. The critical importance of food availability at the initiation of feeding capability was demonstrated 2 days later when fed larvae contain almost 100% more RNA and 55% more protein than larvae held in filtered seawater.

The RNA-DNA ratio was the most reliable and sensitive index of nutritional state evaluated in this study which included relationships between RNA, DNA, protein, standard length, and dry weight. RNA content was the most labile, decreasing within 2 days after removal of food. DNA content was generally conserved except in the final stages of starvation prior to death. The protein-DNA ratio, which is an index of the amount of protein per cell, generally decreased as starvation progressed and the protein-RNA ratio generally increased. The RNA-DNA ratio was particularly useful as an indicator of condition since unlike other indices it fell within well-defined limits throughout most of the period studied. Winter flounder larvae established a mean RNA-DNA ratio of between 4.0 and 4.8 3 wk after initiation of feeding (Figure 2). This range is similar to the RNA-DNA ratio values reported by Bulow (1970) for golden shiners. The RNA-DNA ratio was not greatly affected by either the age or size of the larvae until metamorphosis when the RNA-DNA ratio increased to between 5.3 and 5.7 and remained at this level until the experiment was terminated on day 58 (Table 2). This is particularly important since the age of sea-caught larvae is difficult, if not impossible, to establish and a large size range is observed in larvae of the same age. This point was demonstrated on day 36 when a large mortality of smaller larvae resulted in an increase in the mean DNA, RNA, and protein content of starved larvae. The RNA-DNA ratio, however, was unaffected by the change in size distribution and continued to decrease. Results from larvae transferred to filtered seawater 18 h prior to sampling and allowed to empty their stomachs (Table 1) indicate that the RNA-DNA ratio is not significantly affected by stomach contents at the time of sampling.

The RNA-DNA ratios of winter flounder larvae captured in Narrow River fell within the range of values observed for fed winter flounder in the laboratory. The high RNA-DNA ratios indicated that the larvae were in good nutritional condition. This observation is supported by visual examination of the larvae and the high growth and survival rates of laboratory-reared winter flounder held in situ in Narrow River with a semiopen environmental chamber (Laurence et al. 1979).

Before measurements of RNA-DNA ratios are useful in the field, the effect of changing environmental conditions such as temperature, salinity, and possibly various pollutants as well as low prey concentrations and intermittent feeding should be evaluated. Although adult golden shiners, larval winter flounder, and larval cod, *Gadus morhua*, (Buckley unpubl. data) showed a similar decline in RNA-DNA ratio when food is withheld, the response of other species should be determined.

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EGGS AND EARLY LARVAE OF SMALLMOUTH FLOUNDER, *ETROPUS MICROSTOMUS*

Smallmouth flounder, *Etropus microstomus* (Gill), ranging from early postlarvae to adult were described and illustrated in detail by Richardson and Joseph (1973). Eggs and larvae through yolk-sac absorption had yet to be identified.

During a 1975-76 ichthyoplankton survey of Block Island Sound conducted by Marine Research, Inc. small unidentified planktonic fish eggs were taken. Through subsequent rearing of a number of these eggs and completion of a length series with larger, known larvae, we identified the specimens as *E. microstomus* eggs. Our descriptions of eggs and yolk-sac larvae together with the work of Richardson and Joseph (1973) provide a complete developmental series for identification of this species.

Methods

Sampling was conducted in Block Island Sound at five stations along each of three transects running from Charlestown and East Beach, R.I., to Block Island, a distance of approximately 14.8 km. Collections were made with 60 cm, 0.505 mm mesh, bongo nets. All tows were made obliquely, bottom to surface at approximately 2.5 kn for about 5 min. Digital flowmeters provided volume estimates and quantitative density estimates. Periodically, a 30 cm, 0.505 mm mesh, plankton net was fixed above the bongo net to collect samples of live eggs. These were returned to the laboratory in aerated 4 l thermos jugs and incubated at 20°-21° C. *Etropus microstomus* eggs and larvae were stored in 3-5% buffered Formalin[1] solutions before examination.

Descriptions of the Egg

Etropus microstomus eggs (Figure 1, Table 1) are small, 0.561-0.740 mm in diameter ($\bar{x}$ = 0.64) with a single small oil globule, 0.051-0.165 mm ($\bar{x}$ = 0.12). The egg is spherical with a transparent, unsculptured chorion. The oil globule is also spherical. Occasonally two oil globules were noted or a single one with several surrounding oil particles were found. This condition has commonly been noted for other species (Ahlstrom and Ball

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

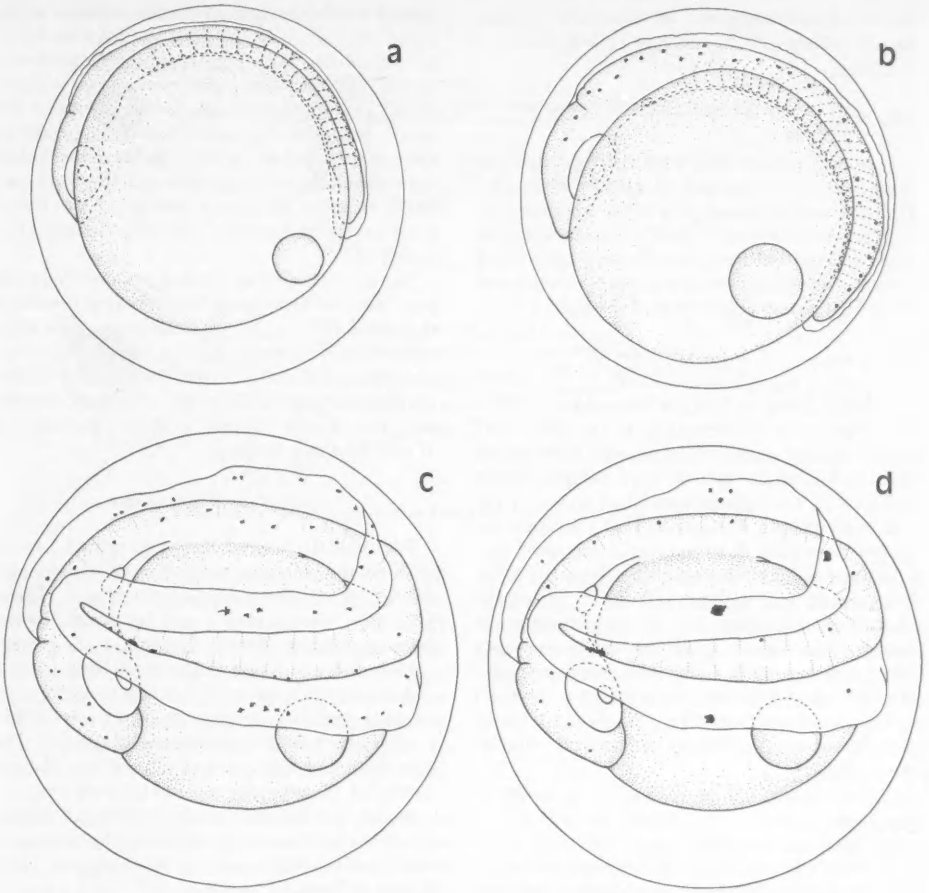

FIGURE 1.—*Etropus microstomus* eggs; mean diameter = 0.64 mm: a) middle stage; b-d) development of pigmentation during late stage.

TABLE 1.—Egg, yolk, and oil globule diameters (millimeters) for *Etropus microstomus* eggs taken in Block Island Sound, 1975.

	Egg diameter				Oil globule diameter				Yolk diameter			
Stage	*n*	Mean	SD	Range	*n*[1]	Mean	SD	Range	*n*[1]	Mean	SD	Range
Early	449	0.64	0.02	0.59-0.73	435	0.12	0.01	0.08-0.17	111	0.52	0.03	0.43-0.59
Middle	261	0.65	0.02	0.59-0.71	257	0.11	0.01	0.05-0.13	239	0.55	0.03	0.49-0.61
Late	111	0.65	0.03	0.56-0.74	102	0.11	0.02	0.08-0.15	103	0.56	0.05	0.49-0.69
Total	821	0.64	0.02	0.56-0.74	794	0.12	0.02	0.05-0.17	453	0.54	0.04	0.43-0.69

[1]Discrepancies in sample sizes resulted from shattered oil globules and yolks which were not measured.

1954; Smith and Fahay 1970; Berrien 1975) and is generally believed to result from shattering during collection or preservation. About 75% of the early stage eggs in our preserved samples also contained broken yolks which could not be accurately measured. To facilitate descriptions, eggs were separated into three stages following Ahlstrom and Ball (1954): early (fertilization to

closure of the blastopore), middle (blastopore closure to tail separation), and late (tail separation to hatching).

Early Stage

During this stage, eggs were distinguishable by measurement of egg and oil globule diameters. The yolk occupied about 81% of the egg diameter. It appeared translucent and yellow-to-amber in color with transmitted, incandescent light. With closure of the blastopore the embryo encompassed about half the circumference of the yolk.

Middle Stage

Faint melanophores began to appear on the dorsal surface of the embryo (Figure 1a). They were widely spaced, appeared randomly distributed, and were easily overlooked at magnifications under 50 ×. No pigment was noted on either the yolk or oil globule. Myomeres (12-22) became visible but were difficult to count with any accuracy. The optic vesicles became clearly visible but lacked pigment. By the end of this stage the number of melanophores increased although they were still present only on the dorsum. In some eggs they began to appear more numerous just behind the head while a few developed on the occiput. As the tail developed free of the yolk material, traces of finfold became visible on the posterior edge of the embryo.

Late Stage

Melanophores enlarged so they became clearly visible (Figure 1b). Some developed along the sides and in some cases a few were noted on the yolk near the embryo. Melanophores along the dorsum commonly migrated into a more or less straight middorsal row extending from the nape to the tip of the tail. As the embryo developed, the portion of this line of pigment posterior to the vent migrated into the dorsal finfold while the lateral melanophores migrated into the ventral finfold (Figure 1c). As this occurred, little pigment remained on the trunk except for the anterior portion of the middorsal row. Numerous small dots persisted on the nape and dorsal surface of the head. Once melanophores had migrated into the finfold they began to coalesce into four distinct spots—two in the dorsal and two in the ventral finfolds; the dorsal pair aligned above the ventral pair. An additional group of melanophores aggregated ventrally near the tip of the notochord (Figure 1d). Much of this pigment spot appeared to be in the finfold but it was always in contact with the trunk and often extended upon it. Some of the small melanophores remaining on the anterior dorsum coalesced and moved into the dorsal finfold approximately midway between the vent and head. In some embryos a portion of the finfold melanophores became dendritic before they coalesced.

The oil globule was located posteriorly in the yolk near the developing vent where it remained through hatching. In some advanced, late stage eggs, one or two melanophores formed on the surface of the oil globule. No additional pigmentation developed on the yolk. Shortly before hatching the embryo encircled the yolk with the tip of the tail almost reaching the snout.

Description of Early Larvae

Two recently hatched larvae measured 1.4 mm NL (notochord length) and were essentially identical to advanced late stage embryos. Three dark spots were present near the margin in the dorsal finfold, two near the margin in the ventral finfold, and one along the ventral body margin near the tip of the notochord. Small melanophores were scattered over the dorsum from the occiput to a point about halfway to the tip of the tail. The eyes remained unpigmented. The oil globule was located at the posterior edge of the yolk sac.

By 2.0 mm NL (Figure 2a) no change in pigmentation had occurred. The yolk was reduced in size by about 50% and the gut and vent more clearly defined.

Specimens >2.0 mm NL were obtained from preserved plankton samples where the finfold and its pigmentation were frequently lost. Between 2.1 and 2.3 mm NL (Figure 2b) the yolk sac was fully resorbed, eye pigmentation developed, and larvae developed many of the characteristics described by Richardson and Joseph (1973) for 2.3-2.5 mm larvae. Melanophores developed along the ventral body margin from the gut to the pronounced spot near the tip of the notochord. As these melanophores developed, most or all of the pigmentation on the dorsum was lost. The distinctive markings in the dorsal and ventral finfolds of yolk-sac larvae remained with the exception of the posterior dorsal spot. This spot was either lost as the caudal band, described by Richardson and

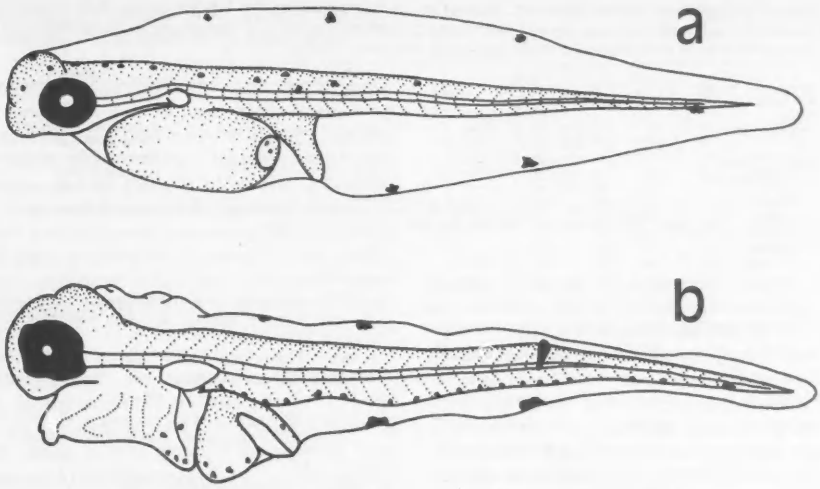

FIGURE 2.—*Etropus microstomus* early larvae: a) 2.0 mm NL; b) 2.2 mm NL.

Joseph, formed or the melanophores migrated ventrally to form all or part of the band. The mid-caudal band was found in larvae as early as 2.1 mm in our collections; it was never observed in larvae still displaying the posterior dorsal finfold spot. The finfold markings appear to have been lost in the 2.5 mm SL (standard length) specimen illustrated by Richardson and Joseph due to finfold mutilation but do appear in their illustrations of 3.5 and 4.5 mm specimens.

The smallest specimen containing pigmentation on the gas bladder in our collections was 2.4 mm. Preopercular spines were first observed at about 2.3 mm. Gas bladder pigmentation and preopercular spines were described by Richardson and Joseph (1973) for their smallest specimen (2.5 mm).

Occurrence

Etropus microstomus eggs were found in our Block Island Sound samples from 11 June until 10 September 1975; sampling was weekly through August, monthly thereafter. Samples taken again on 14 October 1975 did not contain *E. microstomus* eggs. Surface water temperatures during this period ranged from a low of 15.3° C in June to a high of 22.3° C in early August. Larvae were taken from 9 July to 14 October 1975 at which time water temperatures were 15.6° C.

In our weekly 1976 collections, eggs were taken beginning 1 June, larvae beginning 17 June. Both eggs and larvae were found regularly until 26 August when sampling ended. Surface water temperatures averaged 11.9° C on 1 June, 13.2° C on 17 June, and 20.0° C on 26 August.

Similar Species

Prior to formation of the distinctively pigmented embryo in *E. microstomus*, some confusion may occur in separating similar stage eggs of the fourbeard rockling, *Enchelyopus cimbrius*; hakes, *Urophycis* spp.; and butterfish, *Peprilus triacanthus*. According to Scotton et al. (1973), *E. cimbrius* spawns from Nova Scotia to Block Island and *Urophycis* spp. spawn from Nova Scotia to South Carolina, depending upon the species. *Peprilus triacanthus* spawns from Nova Scotia (Scotton et al. 1973) to Chesapeake Bay (Pearson 1941). We regularly collected eggs and larvae of these species in Block Island Sound at the same time that *Etropus microstomus* eggs were taken. Most early and middle stage *E. microstomus* eggs may be distinguished on the basis of their smaller egg and oil globule diameters. Although ranges overlap to some extent (Table 2) mean values for egg and oil globule diameters are fairly distinctive. Only 2% of the 794 eggs we measured contained oil globule diameters ≥ 0.13 mm, the smallest oil

TABLE 2.—Egg and oil globule diameters (millimeters) as reported in the literature for species which might be confused with *Etropus microstomus* eggs. References represent only a portion of those available. Recent literature summaries may be found in Hardy (1978) and Martin and Drewry (1978).

Species	Egg	Oil	Source
Enchelyopus cimbrius	0.65-0.75	0.13-0.15	Battle (1929)
	0.74-0.89 ($\bar{x}$ = 0.82)	0.13-0.20 ($\bar{x}$ = 0.16)	Colton and Marak[1]
Urophycis chuss	0.72-0.76 ($\bar{x}$ = 0.74)	0.15-0.17	Bigelow and Welsh (1925)
	0.62-0.97 ($\bar{x}$ = 0.76)	0.15-0.22 ($\bar{x}$ = 0.19)	Colton and Marak[1]
Urophycis regius	0.67-0.81 ($\bar{x}$ = 0.73)	0.14-0.22 ($\bar{x}$ = 0.18)	Barans and Barans (1972)
Peprilus triacanthus	0.69-0.80 ($\bar{x}$ = 0.75)	0.14-0.22 ($\bar{x}$ = 0.18)	Wheatland (1956)
	0.75-0.79 ($\bar{x}$ = 0.77)	0.17-0.21 ($\bar{x}$ = 0.20)	Colton and Honey (1963)

[1]Colton, J. B., Jr., and R. R. Marak. 1969. Guide for identification of the common planktonic fish eggs and larvae of continental shelf waters, Cape Sable to Block Island. Bur. Commer. Fish. Lab. Ref. 69-9, Woods Hole Biol. Lab., 43 p.

globule diameter reported for the other species. Once pigmentation appears on the embryo, distinction is greatly facilitated. *Enchelyopus cimbrius* and *Urophycis* spp. are easily separated by their heavier and more numerous melanophores. Heavy mealonophores are always scattered on the yolk and oil globule of *Urophycis* spp. while *E. cimbrius* have pigmented oil globules and occasionally pigmented yolk. *Peprilus triacanthus* are somewhat more difficult to separate because, like *Etropus microstomus* they have fine melanophores located on the dorsum. However, this pigment generally forms two distinct rows from the eyes to the tail in *P. triacanthus* and does not migrate into the finfold as it does in *E. microstomus*.

Eggs of Gulfstream flounder, *Citharichthys arctifrons*, may resemble *E. microstomus* eggs since the early larvae are quite similar (Richardson and Joseph 1973). Diameters of unfertilized eggs given by Richardson and Joseph ranged from 0.70 to 0.82 mm ($\bar{x}$ = 0.74) which is considerably larger than *E. microstomus*. Presumably water hardening would increase this diameter even further.

Acknowledgments

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EVIDENCE OF POSTCAPTURE INGESTION BY MIDWATER FISHES IN TRAWL NETS

The ingestion of food items by midwater fishes in trawl nets, if it occurs at appreciable levels, may pose serious bias problems for dietary studies based on stomach content analyses. In a recent discussion of "net feeding," Hopkins and Baird (1977) reviewed the available evidence and found that while it may occur to some degree, net feeding is probably not extensive. In an earlier field study, Hopkins and Baird (1975) used side-by-side nets that provided captured fishes with different levels of exposure to captured zooplankton. On one side the fish were allowed to enter the cod end of the net and mingle with the zooplankton concentrated there. In the adjacent net fishes were excluded from the cod end by an 11 mm mesh bag at its mouth. Their results from 19 intraspecific comparisons of 700 myctophid and gonostomatid fishes showed little significant data that indicated net feeding.

All of the evidence to date, both for and against postcapture ingestion, has been indirect. This is because there was no sure way to determine whether a food item had been ingested in the net. The following study was conducted in order to provide a more direct investigation of stomach content contamination.

Methods

Experiments were conducted by introducing bogus food items into the cod end of a net before launching it, and then examining the stomach contents of captured fishes after recovery. Eleven such hauls were made with Tucker-type midwater trawls in deep water off southern California (Table 1). The nets had a main scoop of 6 mm nylon mesh and a rear section of 0.333 mm plankton netting. The 9 m^2 net utilized an enclosed, bag-type cod end (Baker et al. 1973) on two hauls (10, 11) and a rigid closing cod end (Childress et al. 1978) on three hauls (7, 8, 9). Both of these cod ends are of the flow-through variety and allow the passage of water out the rear. The 2.3 m^2 net had a rigid, nonclosing, 3.7 l plastic jug cod end that restricted flow.

Prior to launching the trawl, approximately 100 ml (or about 3,000 pieces) of artificial prey were placed in the cod end. In all cases, the amount of bogus prey introduced was much less than the eventual catch of similarly sized zooplankton in the cod end. The material consisted of rubber band fragments and bits of filter paper, between 2 and 15 mm in greatest dimension. Their individual volumes ranged between 0.5 and 60 mm^3, which falls within the size range of natural prey items. Upon recovery, the cod end samples were preserved initially in 10% formaldehyde then transferred to 50% isopropanol. In the laboratory, fish stomachs were removed from the body cavity before being opened for examination. Only material from intact stomachs was counted, material found in the mouth and esophagus was not recorded. Data from haul 23 are biased toward larger individuals because the smallest specimens in the catch were not examined. Percent net feeding represents the relative number of individuals of any species which had ingested at least one bogus prey item. It is necessarily a conservative representation because zooplankton from the cod end may also have been ingested after capture but could not be distinguished from naturally ingested prey.

TABLE 1.—Trawling data for the ingestion experiments at Santa Barbara (SB) and San Clemente (SC) Basins, and off Guadalupe Island (GI), Calif.

Haul no.	Date 1977	Location	Mouth opening (m^2)	Day/ night	Depth (m)	Duration (min)
1	Apr. 12	SB	2.3	N	0-190	60
2	12	SB	2.3	N	0-130	50
3	13	SB	2.3	N	0-150	50
4	13	SB	2.3	D	0-500	95
5	14	SB	2.3	D	0-400	100
6	14	SB	2.3	D	0-590	145
7	Feb. 22	SC	9	D	0-425	80
8	22	SC	9	Evening	483-891	180
9	24	SC	9	D	526-634	165
10	Aug. 10	GI	9	D	450-480	90
11	13	GI	9	N	0-150	135

Results

A total of 1,211 specimens were examined, representing 15 midwater fish species. Fifty-nine individuals (5% of the total) from 10 species were found with artificial prey in their stomachs (Table 2). Most of the bogus prey ingested (92%) were small (0.5-6 mm^3) and only four fish had swallowed artificial items >12 mm^3. Generally, the average number per stomach was low (Table 2) but a few fish had their stomachs packed with artificial prey. Only 5 of the 59 fishes containing bogus prey had stomachs which were otherwise empty; all others also contained zooplankton, some portion of which may have been ingested in the cod end.

Notable differences in net feeding occurred both interspecifically and intraspecificaliy. The two

TABLE 2.—Occurrence of bogus prey items in the stomachs of midwater fishes. Sizes are standard lengths in millimeters.

Species	No. of fish	Mean size (range)	Fish that net fed			Mean no. bogus prey	% net fed night/day
			Number	Percent	Mean size		
Bathylagus wesethi	35	50(27-84)	0	—	—	—	—
Leuroglossus stilbius	20	60(45-100)	1	5.0	100	1.0	0/100
Cyclothone acclinidens	64	45(26-57)	1	1.6	56	1.0	—
C. signata	89	20(17-38)	0	—	—	—	—
Poromitra crassiceps	6	44(34-75)	1	16.7	75	3.0	—
Scopelogadus m. bispinosus	13	55(43-69)	0	—	—	—	—
Lampanyctus ritteri	14	77(39-100)	7	50.0	68	3.8	0/50
L. regalis	15	42(35-53)	0	—	—	—	—
Parvilux ingens	11	71(35-172)	0	—	—	—	—
Stenobrachius leucopsarus	138	52(24-82)	32	23.2	61	2.3	5/47
Symbolophorus californiensis	6	48(30-62)	2	33.3	60	3.5	0/67
Triphoturus mexicanus	742	56(19-67)	11	1.5	50	1.2	1/2
Ceratoscopelus townsendi	22	42(33-48)	2	9.1	44	19.5	0/100
Sternoptyx diaphana	20	29(14-37)	1	5.0	37	1.0	0/7
Idiacanthus antrostomus	16	175(63-318)	1	6.3	231	1.0	0/25
Total	1,211		59				

TABLE 3.—Haul by haul comparisons of postcapture ingestion by *Stenobrachius leucopsarus*. Measurements are standard lengths in millimeters.

Item	Nighttime hauls		Daytime hauls		
	1	2	4	5	6
Number of fish examined	48	25	21	26	13
Mean size (range)	46(26-68)	50(30-81)	60(32-79)	53(34-70)	51(36-69)
Number net fed	3	1	12	10	6
Percent net fed	6.3	4.0	57.1	38.5	46.2
Mean size net fed	54	59	64	59	60
Number of fish ≥51 mm	23	15	19	17	11
Percent fish ≥51 mm net fed	13.0	6.7	63.2	58.8	54.5
Mean number bogus prey/stomach	1.3	1.0	2.0	3.4	1.7
Number of fish net fed/hour	3.0	1.25	7.5	5.9	2.5

most abundant fishes in the collection, myctophids *Stenobrachius leucopsarus* and *Triphoturus mexicanus*, showed a large difference in the percentage of individuals which had ingested the bogus prey items (23.2% vs. 1.5% respectively). In 8 of the 10 species that showed net feeding, larger-than-average individuals were more likely to contain artificial prey than smaller ones.

A haul by haul comparison of data on *S. leucopsarus* (Table 3) shows a greater degree of net feeding in daytime hauls than at night; although the average size of specimens in nighttime hauls is smaller (t-test, $P<0.001$). If we consider only those specimens which were equal to or larger than the smallest individual found with bogus prey in its stomach (51 mm), the trend for greater daytime net feeding still holds. All other species also showed a higher incidence of daytime net feeding (Table 2).

Discussion

The ingestion of bogus prey items by midwater fishes is direct evidence that the contamination of stomach contents can and does occur in the cod ends of midwater trawls. The degree to which it occurs, and thus the seriousness of the bias imparted to dietary studies, is apparently variable. Within a collection of midwater fishes, our data and that of Hopkins and Baird (1975, 1977) indicate that overall the bias may be low. However, the data from the present study showed that important levels of contamination can occur within some species. Hopkins and Baird (1975) based their low estimates of net feeding on intraspecific comparisons of their paired net data. The same data, when examined interspecifically, reveals that in 14 of 19 comparisons (700 fish from 11 species), fishes prevented from reaching the cod end had a lower average number of prey items in their stomachs than fishes which had entered the cod end. The probability of finding no difference in the number of prey items between these samples (i.e., no net feeding) is <10% (Wilcoxon matched pair signed rank test); thus their data indicating net feeding is significant to at least the 90% level of confidence.

Several factors may be responsible for the observed variations in degree of net feeding. The condition and viability of captured fishes is certainly a key factor; hardy species such as *S. leucopsarus* and *Symbolophorus californiensis* commonly survive capture and arrive at the surface alive and active. The survival of other fishes

(e.g., *T. mexicanus, Cyclothone acclinidens, C. signata, Sternoptyx diaphana*) is usually quite low. Obviously a dead fish cannot swallow cod end material while a stressed but living fish may. The survival factor may have caused some of the differences between our results and those of Hopkins and Baird (1975); off California the survival rate of trawled specimens is relatively high (Childress et al. 1978) while in the Gulf of Mexico it is very low (T. L. Hopkins and R. C. Baird, pers. commun.). Survival rate is probably influenced by haul duration, the depth and temperature range sampled, cod end design, and net construction.

It is also apparent that specimen size can influence the degree of net feeding. It is not clear whether this is due to the greater survival rate of larger individuals or to their larger mouth size. Within the limits of survival rate and size variables, the degree of exposure to prey in the cod end is a function of haul duration, the depth strata sampled, and the amount of time a fish spends in the cod end. Discrete-depth hauls probably decrease the degree of exposure by limiting the number and diversity of prey items while oblique hauls increase exposure. The data also indicate that small prey are more readily ingested in cod ends than large prey. Accordingly, the bias imparted to stomach content analyses by net feeding would be toward the smaller prey items.

Postcapture ingestion is a complex problem and no clear-cut conclusions can be drawn from the available data except that it occurs to a varying degree and that the extent of its occurrence is subject to fish survival, fish size, and exposure. To gain a predictive capability it will be necessary to investigate these factors further.

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INHIBITORY EFFECT OF THE ALGA *PAVLOVA LUTHERII* ON GROWTH OF MUSSEL, *MYTILUS EDULIS*, LARVAE

The culture of bivalve larvae sometimes appears to be more of an art than a science. Many factors can influence the growth and survival of larvae and it is usually difficult to assign a cause to the failure of a particular culture. In one instance we had set up a large experiment with mussel, *Mytilus edulis*, larvae and noticed after 5-8 days that the larvae had ceased to grow in all of our treatments but that they remained alive and active. During this experiment one factor was known to have been changed: Previously we had been feeding the larvae a mixture of the algae *Isochrysis galbana* and *Pavlova lutherii*, while in this experiment only *P. lutherii* was available.

There has been one account in the literature (Fretter and Montgomery 1968) of *P. lutherii* being toxic; yet Bayne (1965) found *P. lutherii* to support normal growth in *M. edulis* larvae. Davis and Guillard (1958) found *P. lutherii* to be as good as *I. galbana* (and about as good as a mixture of the two) when fed to larvae of *Crassostrea virginica* and *Mercenaria mercenaria*. The results of Wilson (1978) show that *P. lutherii* is as satisfactory as other algae as food for *Ostrea edulis* larvae. In order to determine whether our *P. lutherii* cultures were to blame for the lack of growth we observed, we set up an experiment to compare the growth of mussel larvae when fed several diets of algae.

While testing the species of algae, we decided to include different food levels. If *P. lutherii* were toxic, then its effects may increase with concentration of the algae given to the larvae. Another source of toxic substances could be the algal metabolites which accumulate in the algal cultures. In order to test this, we used two different sources of *P. lutherii*, a young culture and an old one. Bayne (1965) had observed a slightly better growth of *M. edulis* larvae when fed *P. lutherii* from a 4-day-old culture compared with those fed a 13-day-old culture.

Methods

Adult mussels were stimulated to spawn by raising the water temperature from an ambient of 15° C to 22°-24° C. The eggs and sperm from five females and seven males were pooled to give a heterogeneous population of larvae. After 2 days the larvae were placed in the various treatment combinations. In the experiment there were five combinations of algae: a) *Isochrysis galbana* alone; b) *I. galbana* plus *Thalassiosira pseudonana* (added after 1 wk); c) *I. galbana* and *P. lutherii* throughout, plus *T. pseudonana* after 1 wk; d) a young culture of *P. lutherii* harvested 4-7 days after innoculation, and e) an old culture of *P. lutherii* harvested 14-20 days after innoculation. In the mixed algae treatments the two or three species were added in equal proportion by cell number.

There were three feeding protocols used. Cell concentrations were increased gradually over the first week of growth, and although the cell concentrations changed in each protocol they will be referred to as "levels" here for simplicity. The food levels used were: 1) 10,000 cells/ml throughout the experiment; 2) 10,000 cells/ml from day 2 to day 4, 15,000 cells/ml from day 4 to day 6, and 20,000 cells/ml for the rest of the experiment; and 3) 50,000 cells/ml from day 2 to day 4, 100,000 cells/ml from day 4 to day 6, and 500,000 cells/ml for the rest of the experiment.

TABLE 1.—Analysis of variance on size of *Mytilus edulis* larvae as related to food treatment. Analysis performed on mean larval length for 6 replicates per treatment combination.

Source of variation	df	Mean square	F
Food level	2	2,477.2	24.7**
Food type	4	5,952.9	59.35**
Food level × food type	8	307.1	3.06**
Residual	75	100.3	

**$P<0.01$.

There were 6 replications in 1 l beakers at each of the food type-food level combinations. All beakers were held at 15° C. The initial density of the larvae at day 2 was 20 larvae/ml. All beakers were sampled when the larvae were 16 days old and up to 10 larvae were measured from each beaker.

Results

The main source of variation in the larval lengths at day 16 was due to the food type, with a smaller but significant portion attributable to the food level and the interaction of these two effects (Table 1). The largest source of variation among the types of food was the difference between the larvae fed only *P. lutherii* and those fed the other food types (Figure 1). There was slightly better growth with the young *P. lutherii* as food at the

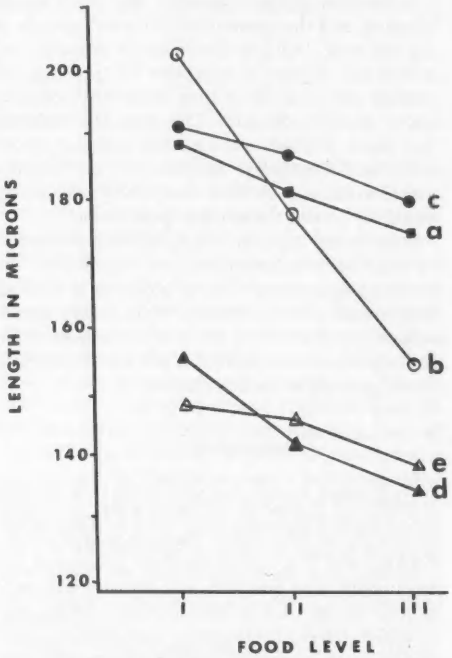

FIGURE 1.—Mean size of mussel larvae at 16 days when grown at three different algal food levels and on five combinations of algal types: a) *Isochrysis galbana* only; b) *I. galbana* and *Thalassiosira pseudonana*; c) *I. galbana*, *T. pseudonana*, and *Pavlova lutherii*; d) young *P. lutherii*; and e) old *P. lutherii*. Means are based on 10 animals from each of 6 replicates at each of the treatment combinations. See text for description of food levels used.

lowest food level compared with the old culture. The interaction of food level and food type was probably in large part due to food type b (*I. galbana* and *T. pseudonana*), which gave the best growth at food level 1 but poor growth at food level 3.

The effect of the food level was to produce higher growth rates at the lower food concentrations. This occurred for all five food types (Figure 1).

Discussion

Contrary to published reports on various bivalve larvae (Guillard 1959; Bayne 1965; Wilson 1978), we have observed poor growth of *M. edulis* larvae when fed only *P. lutherii*. This was true at all three food levels tested and whether the *P. lutherii* culture was young or old. There was no apparent inhibitory effect by the *P. lutherii* on larval growth when fed in combination with the other two algal species. It would appear that the suppression of growth of the larvae when fed only *P. lutherii* was the result of a dietary deficiency. If it were due to toxins in the algal cells, one would expect to see a greater suppression of the growth rate in the larvae at food level 3 when *P. lutherii* was combined with the other algal species.

If the inhibitory effect of *P. lutherii* were primarily due to the accumulation of metabolites in the medium, there should be a more consistent difference between the *P. lutherii* cultures of different age. In fact, there was only a small difference at food level 1. This may indicate that there is some effect of metabolites which were in low enough concentration in the young culture to be diluted at food level 1 but not at the other food levels. Nevertheless, it appears that the main effect of *P. lutherii* is or is equivalent to a dietary deficiency. This could be due to the biochemical compostion of the algal cells such that they are not digested, lack of some essential nutrient, or are not even ingested. The cells are not much bigger than *I. galbana*, especially when fast growing, and there was no evidence of clumping of the cells into large aggregates.

There is some evidence in the data presented by Davis and Guillard (1958) and Bayne (1965) of a suppression of larval growth at high concentration of *P. lutherii*. But to our knowledge there are no reports of suppression of growth in bivalve larvae at lower concentration of *P. lutherii*. This algae has been reported as producing substances toxic to four species of prosobranch larvae (Fretter and Montgomery 1968). Apparently, a toxic substance is emitted by the algae, which accumulates in the algal culture.

The results of the different food levels are not new (Davis and Guillard 1958; Bayne 1965; Rhodes and Landers 1973). The purpose of using different food levels in this experiment was to look for interaction with food type.

At this point we can only speculate as to the reasons for the lack of growth of larvae fed *P. lutherii*. We would not want to generalize and say that all *P. lutherii* could produce the same results. Obviously others have obtained good results with their cultures. (All our algal cultures are grown in the f/2 medium of Guillard (McLachlan 1973), which is commonly used in growing algae for shellfish culture.) One explanation would be that we have inadvertently developed through genetic change a strain of *P. lutherii* which is of inferior quality. Fretter and Montgomery (1968) have suggested that bacteria can metabolize the toxic substance produced by *P. lutherii* and render the algae culture harmless to bivalve larvae. Perhaps the absence of bacteria in our *P. lutherii* cultures, or at least the appropriate bacteria, would explain the discrepancy between our results and others. Unfortunately, we did not check the algal cultures for the presence of bacteria.

The importance of our observations with *P. lutherii* need to be assessed by other workers. The culture conditions of algae will vary from lab to lab and could easily have an influence on the growth of bivalve larvae.

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